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SERIE: PLANKTON · BIND IV

NR. 1. GUNNAR THORSON: REPRODUCTION AND LARVAL DEVELOPMENT OF DANISH MARINE BOTTOM INVERTEBRATES, WITH SPECIAL REFERENCE TO THE PLANKTONIC LARVAE IN THE SOUND (ØRESUND)

KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI A/S
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REPRODUCTION AND LARVAL DEVELOPMENT OF DANISH MARINE BOTTOM INVERTEBRATES,

WITH SPECIAL REFERENCE TO THE PLANKTONIC LARVAE IN THE SOUND (ØRESUND)

BY

GUNNAR THORSON
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(WITH A SECTION ON
LAMELLIBRANCH LARVAE BY C. BARKER JØRGENSEN)

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1946

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TO THE MEMORY OF
C. G. JOH. PETERSEN

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I. Introduction.

The Danish waters have been rather thoroughly investigated. From the time when Ørsted (1844) published his "De regionibus marinis" and up to the present year Danish biologists have taken a great interest in marine biology. The cruises of the gun-boat "Hauch" in 1883—86 secured large collections, which were of great importance, especially as regards the fauna of invertebrates, and when in 1889 Dr. C. G. Joh. Petersen was appointed leader of the newly founded "Dansk Biologisk Station", it was a matter of course that the fauna of invertebrates was included in his investigations. During the ensuing 30 years Petersen, Boysen-Jensen, and Blegvad have gone into these problems in several papers. This work culminated in the years 1911—1915, when Petersen and Boysen-Jensen published their well known "Animal Communities of the Sea Bottom" and by the aid of the newly constructed bottom sampler — "the Petersen grab" — secured large series of quantitative samples from the Baltic to the Skagerrak. This detailed charting of the bottom animal communities in the Danish waters has been of fundamental value for future investigations here. However, Petersen has never given any definition of his animal communities, a fact which has led to several misapprehensions, because other scientists have regarded them as identical with biocoenoses — an interpretation which differs entirely from that of Petersen himself (cf. the discussion by Spärck 1937). The relation between an animal community and a biocoenosis, however, cannot be solved, until we have acquired a detailed knowledge of the biology of each single species of invertebrate living in a "community", and until we have cleared up their requirements as regards food, salinity, temperature, substratum, surrounding animals, and — above all — their breeding habits and mode of larval development. McGinitie (1932, 1939) has recently emphasised the necessity of such an analysis, and in an exceedingly interesting paper Remane (1933) has proved the correlation between bottom-type (sand, clay, vegetation) and animal-type (size, shape, ciliation, mode of locomotion, sessility, mode of feeding, etc.) in the fauna of the Bay of Kiel. Further, Thamdrup (1935), Wohlenberg (1937), Linke (1939) and other authors have analysed the fauna of the tidal zone, where the conditions for such an analysis are, of course, much more favourable than in deeper water.

Petersen also intended to enter further into the biological details regarding the members of his animal communities. Here his interest was chiefly focussed on the breeding habits of the bottom invertebrates, because the settling of larvae and the growth of young specimens was of fundamental importance for his final aim, which was to acquire knowledge of the production of the sea bottom, i. e. the quantity of "fish-food" produced every year. The still more intimate connection between "Dansk Biologisk Station" and the practical fishery industry, however, has necessarily caused these detailed breeding investigations to be neglected for the benefit of more urgent studies on the fishes themselves, and it can hardly be expected that the station will find time to take up the work for the present.

The aim of the present investigation is, then, to continue the analysis of the Danish bottom invertebrates, especially of their breeding habits, but instead of concentrating on the young bottom stages, it will be attempted to trace the species back to the planktonic larval stages and enter into problems associated with the development and the pelagic larval life. As soon as we are able to identify and recognise the pelagic larvae in our seas, it will be possible by the aid of regular plankton hauls throughout the year to ascertain the breeding season of by far the majority of our bottom invertebrates, and it then seems possible to consider the results gained from an ecological point of view, i. e. to study for instance spawning, larval occurrence, larval metabolism, food demands, growth and waste during the planktonic life, etc., in relation to temperature, salinity, food conditions, enemies, etc. If we use these methods on a sufficiently large material and for a couple of years in suitable localities, it seems likely that the first rough outlines of the problems concerning the ecology of pelagic bottom animal larvae will suggest themselves.

As mentioned above, these problems are of fundamental importance for the analysis of the character of marine animal communities. The breeding season and larval development comprise the most sensitive periods within the whole life of most of these animals. Species able to vegetate at rather low temperatures require very definite and normally much higher temperatures to ripen their sexual products and to spawn them (ORTON 1920). The youngest cleaving stages of several marine invertebrates need much more precise and limited temperature intervals than those which are necessary for older larvae and bottom stages (PELSENEER 1901, S. RUNNSTRÖM 1927 a). Spermatozoa in Echinoderms are extremely sensitive to changes in salinity and pH, and rather a high salinity and a high pH are necessary to make them active (MORTENSEN 1921, 1937, 1938, HÖRSTADIUS 1925). The content of phytoplankton seems on certain occasions to be the factor which starts or retards the spawning of a whole stock of marine invertebrates (MIYAZAKI 1938c, and this paper pp. 423—424); the amount of food required by larvae of bottom invertebrates is 5 to 10 times larger than that of their parents on the bottom (ZEUTHEN, cf. this paper p. 459), etc. The breeding seasons are normally the critical stages — the "eye of a needle" — during the whole life of most marine bottom invertebrates, and the conditions prevailing in a particular locality during the ripening and spawning and during the development of the larvae will normally be decisive for the occurrence or non-occurrence of each species within the locality.

In the literature on marine plankton, bottom animal larvae have been almost totally neglected even in fairly large and thorough surveys, cf. e. g. AURIVILLIUS (1898 a), PETERSEN (1897, 1903), SØREN JENSEN, JOHANSEN and LEVINSEN (1903), BIGELOW (1928) and DAKIN & COLEFOX (1933). All that can be gained from these papers is a few remarks on "molluscan larvae" or "annelid larvae", etc., taken as a whole, and for our purpose such information is of little value, if of any value at all. AURIVILLIUS's (1898 b) and MARIE LEBOUR's (1917) attempts to include the bottom animal larvae in their lists of the plankton from Bohuslän and Plymouth respectively show very strikingly the almost total lack of knowledge of the larvae. Within Lamellibranch larvae, as within Prosobranch larvae, most of the species are very similar to each other, and the scientists who have had to work up a whole fauna from a large number of plankton samples had to neglect them, unidentified as they were. If the samples are preserved in alcohol or formalin, the preservation of bottom animal larvae will normally be so poor that every attempt at an identification on preserved material will be in vain; the larvae must be examined in a living state, and may then later on be recognised in fixed samples also. The identity of even the commonest larvae has been dubious or totally unknown up to recent years.

Thus, the eggs and larvae of *Littorina littorea* were identified as late as 1911 (Caullery & Pelseneer), those of *Turritella terebra* and *Aporrhais pes pelecani* in 1933 a (Lebour); the larva of *Arenicola marina* was first described in 1923 (Blegvad), the larva of *Cardium edule* in 1938 (Lebour), and that of *Macoma baltica* in 1939 (Werner). The larvae of such common forms as for instance *Aphrodite aculeata*, *Cyprina islandica*, and *Syndosmya nitida* are still unknown.

During the last fifteen years, however, our knowledge of bottom animal larvae in the plankton has been considerably increased, especially owing to the works of Mortensen (Echinoderms), Lebour (Prosobranchs, Lamellibranchs, Decapods), and D. P. Wilson (Polychaetes). However, these authors, which have supplied excellent contributions to our knowledge of the individual groups of larvae, have not hitherto used their experience to present a synthesis from an ecological point of view, e. g. on the spawning and development in a larger systematic group all the year round within a limited area, in relation to temperature, salinity, food conditions, etc. The only attempt made to follow the larvae of a whole group throughout a year within a limited area and to identify them, is, as far as I am aware, that of Aiyar (1933) on the Annelid larvae from the Madras coast.

Thus our investigation has a double purpose: to identify and sketch as many planktonic bottom animal larvae as possible, and from the occurrence of these larvae in the plankton throughout the year to form a picture of the breeding season and, when possible, the length of the larval life, the "breeding intensity", and the waste of larvae, etc., for each single species within the area investigated.

To identify all larvae before studying their occurrence and numbers during the varying seasons would mean a loss of time. The two branches of the survey had to proceed simultaneously, and the following programme was therefore planned:

A. Collecting of regular plankton hauls ("main series") representing the whole water mass from the bottom to the surface, together with hydrographical measurements every fortnight throughout the year from fixed stations ("main stations") in suitable localities.

B. Such conditions must be established that the plankton samples collected could be thoroughly studied in a living state.

C. Each larval form secured must be separated from the other forms, the number of specimens must be counted, and the larvae, after being carefully sketched by means of an Abbe drawing apparatus, must be provided with a provisional name, under which it must be inserted in the lists.

D. Such larvae as for instance small Lamellibranch larvae, Polychaete-Trochophores, etc., which could not be separated into distinct species, must also be mentioned in the lists, so that every list comprises all bottom animal larvae taken in a main series on the particular date.

E. The larvae sketched and provided with names must gradually be identified as soon as possible, in order that the provisional names in the lists could be replaced by their real names.

As "suitable localities" the northern and middle parts of the Sound were chosen. The whole survey has been carried out in our leisure hours, and the locality must therefore necessarily be situated as near Copenhagen as possible. The Sound has many advantages. Consisting of a north-going brackish Baltic surface layer and a south-going salt Kattegat layer along the bottom, often with a very distinct spring layer between (cf. the hydrographical remarks on pp. 23—25), it gave us the chance to work with "Baltic larvae" and with "Kattegat larvae", each of the two water layers having its own special larval stock. Accordingly the Sound comprises the majority of all fauna elements and animal communities from both these neighbouring areas. Thus the Sound from Gilleleje—Kullen in the north to Amager—Limhamn in the south harbours at least 32 species of Echinoderms, 142 Polychaetes, 69 Prosobranchs, 41 Opistobranchs, and 61 Lamellibranchs. PETERSEN (1913, p. 14) mentions the Sound as "..... representing all the faunas or communities found in the Belt Sea restricted within the narrow channel between Elsinore and Copenhagen".

The pronounced brackish surface water and the much salter water in the deeper layers of the Sound cause a remarkable "vertical concentration" of the fauna. At depths ranging from 15 to 35 m the Sound comprises a stock of species nearly similar to that which occupies the areas from the tidal zone to a depth of about 70 m e. g. off N.E. Jutland and Bohuslän. The exceptionally large number of species (for several groups more than double the number known from the Great Belt), the many different animal communities within a limited area, the separate stocks of larvae within the two different water layers with different salinity, entirely different seasons for maximum and minimum temperatures, and quite different amounts of phytoplankton, render it possible for the biologist to combine and choose just those factors the influence of which are of special importance for each step of his survey.

Acknowledgements.

A survey like the present which extends over several years and is carried on from two laboratories in two different countries, with several biologists assisting, and partly during the great war, cannot, of course, be carried through without the author receiving help from many quarters.

The greater part of the expenses of the publication of this paper and the main expenses for the whole investigation have been defrayed by the Carlsberg Foundation, the latter by annual grants from 1936 up to the present year. The Rask-Orsted Foundation has rendered possible a correction of the English manuscript. Smaller amounts have been placed at my disposal by JAPETUS STEENSTRUP's Legat.—LAURITS ANDERSEN's Fond, the Tuborg Fond, and the D. D. P. A. Fond have rendered financial aid for the practical part of the investigation (dealing with the growth of "fish-food"), and have thus also supported the scientific work. To all these funds I express my sincerest thanks.

The Lord mayor of Helsingør, PEDER CHRISTENSEN, and the municipal council of that town have with great understanding and interest placed laboratory premises at our disposal, when war conditions suddenly forced us to transfer the regular survey from Ven (Sweden) to the Danish coast.

The Royal Danish Navy, represented by J. JEGSTRUP, commander R.N., and KAI BANG and IVER WESTERGAARD, lieutenants R.N. reserve, have given excellent help in placing patrol-boats at our disposal during the work off Helsingør.

When we established the laboratory at Ven, I received valuable help from the Rev. PAUL LINDBERGH and the consistory there, and from the Chapter in Lund, which placed a site at my disposal.—Further, Prof. BERTIL HANSTRÖM and Prof. TORSTEN GISLÉN, both of Lund, have helped me to obtain a permit to visit Sweden even during periods when this was extremely difficult.

Prof. Dr. phil. AD. JENSEN and Dr. phil. TH. MORTENSEN have taken a special interest in my work and have given me much good advice. Dr. phil. H. BLEGVAD, chief of the Danish

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My mother, Mrs. Astrid Thorson, and my wife, cand. mag. Mrs. Ellen Thorson, have done their utmost during the summer surveys at Ven to invest the functionalistic laboratory with the comforts of a home and to enable us to combine the scientific work with splendid summer holidays.

Mrs. E. Gleerup has corrected and revised the English manuscript.

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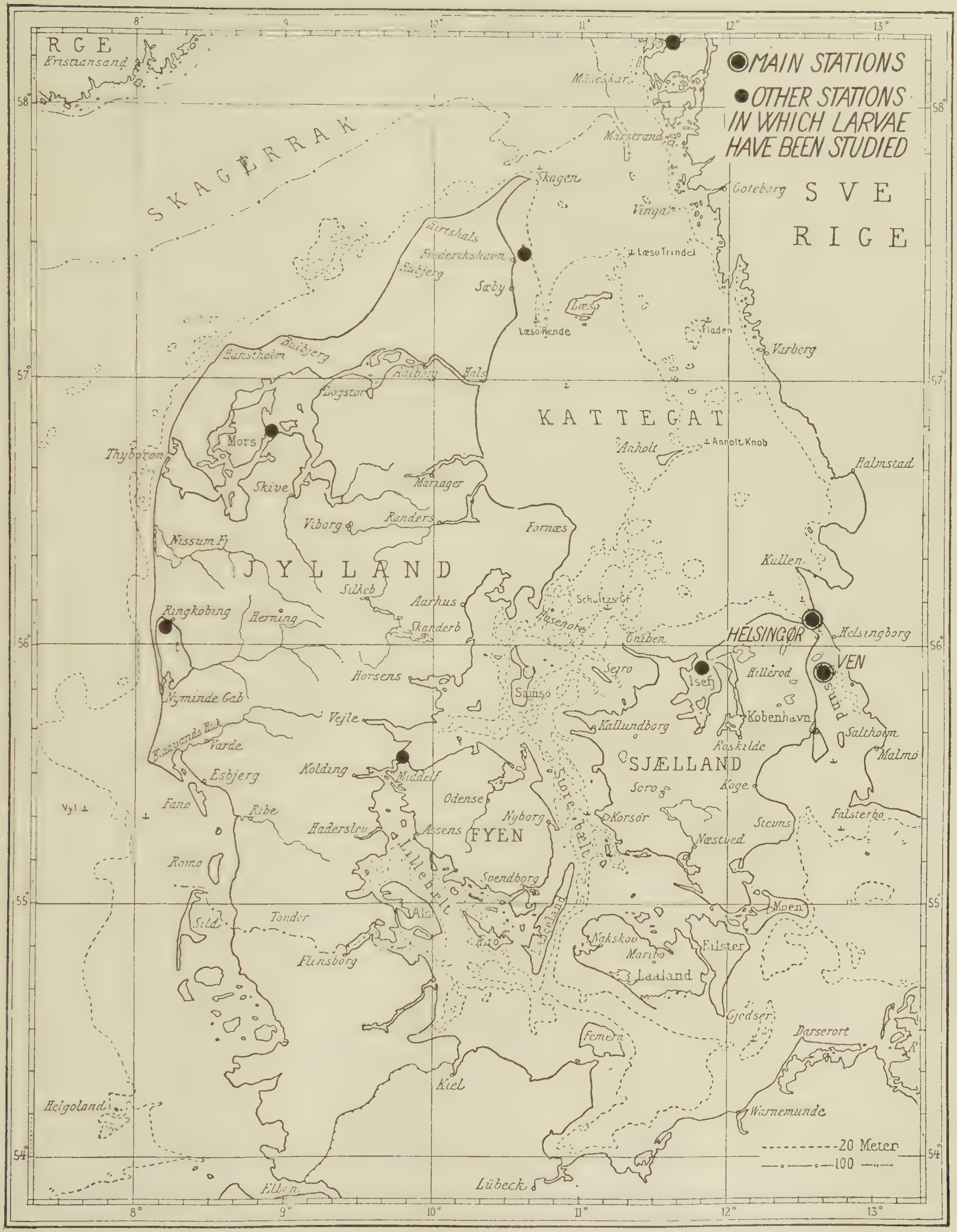

MAIN STATIONS
OTHER STATIONS IN WHICH LARVAE HAVE BEEN STUDIED
SKAGERRAK
KATTEGAT
JYLLAND
FYEN
SJÆLLAND
SVERIGE
RGE
Kristiansand
Skagen
Hirtshals
Frederikshavn
Sæby
Læsø
Læsø Rende
Læsø Trindel
Göteborg
Vinga
Marstrand
Varberg
Fladen
Anholt
Anholt Knob
Halmstad
Kullen
HELSINGØR
Helsingborg
VEN
Hillerød
København
Saltholm
Malmö
Isefj
Roskilde
Køge
Falsterbo
Stevns
Næstved
Sorø
Korsør
Kallundborg
Sejrø
Gniben
Schultzs Gr
Samsø
Hasenøre
Aarhus
Skanderb
Silkeb
Horsens
Vejle
Kolding
Middelf
Odense
Nyborg
Assens
Haderslev
Svendborg
Als
Ærø
Langeland
Lillebælt
Storebælt
Øresund
Nakskov
Maribo
Laaland
Falster
Moen
Gjedser
Darserort
Warnemünde
Lübeck
Kiel
Femern
Flensborg
Tønder
Sild
Rømø
Ribe
Fanø
Esbjerg
Varde
Blaavands Huk
Nymindegab
Ringkøbing
Herning
Viborg
Randers
Mariager
Fornæs
Skive
Mors
Thyborøn
Nissum Fj
Hanstholm
Bulbjerg
Løgstør
Aalborg
Hals
Vyl
Helgoland
Elben
8°
9°
10°
11°
12°
13°
54°
55°
56°
57°
58°
20 Meter
100

Fig. 1. Map of Denmark and adjacent waters showing the localities in which the reproduction and larval development have been studied for the present paper.

A. The net hauls. After the boat had anchored at the fixed station, the temperatures in the water column had to be ascertained in order to find the depth of the spring-layer. Temperatures were measured by means of a MARTIN KNUDSEN water-sampler at the surface, at depths of 5 m, 10 m, 15 m, and directly over the bottom, viz. at a depth of 18 m. Our original plan, viz. to secure a series of water samples every fortnight in order to ascertain the exact salinity, was abandoned, because owing to our primitive equipment and the stormy weather during the whole winter half-year this proved impossible if the main purpose—the collecting of plankton series—was also to be carried out. A careful hydrographic survey has, however, been planned for the years to come.—The next point was to secure a large water-sample from a depth of about 15 m (off Ven) or 30 m (off Helsingor), as experience has shown that most of the planktonic larvae will thrive much better in this water than in surface water. After this water had been poured into Dewar vessels, the plankton hauls were taken. The main series included 10 samples each from the bottom to the surface, taken with a small conical net (25 cm in diameter at the mouth, about 50 cm deep, ending in a plankton-pail with a leaden weight; gauze No. 12, i. e. 12 meshes per mm), which has proved sufficiently fine to catch all stages of planktonic larval invertebrates in the Sound, probably apart from certain larvae of Sponges. These 10 samples collected in Dewar vessels form the main basis of our investigation. Besides this, supplemental series were taken with a somewhat larger net, 35—40 cm in diameter, and during the whole summer and, when time could be afforded for it, in winter, too, supplemental series were secured the following day also, in order to avoid a generalisation based upon samples from a single day.

On arrival in the laboratory the samples were pipetted up into Petri dishes and assorted into main groups. Afterwards, the individual groups were counted, and sketches drawn, one zoologist especially studying Polychaete larvae, another Lamellibranch larvae, and so on, and in this way the whole content of a main series was noted down in a list with additional remarks on temperatures, currents, contents of phytoplankton, etc. Such main series are available from Ven from every two or three weeks from August 1936 to August 1939—a period long enough to give a reliable picture of the main variations from year to year; as mentioned above, they have been supplemented by similar series from Helsingor from the period September 1941 to September 1942.

B. The pump series. In order to ascertain the vertical distribution of the bottom animal larvae within the water column, the collection of pump series was commenced off Ven in the summer of 1937. The jolly-boat, provided with an ordinary wing-pump to which was attached a 20 m long hose with a leaden weight at the end, was anchored at our fixed station. From each metre of the water column, from the surface to about 25 cm above the bottom, 200 l of water were pumped up and filtered through a plankton sieve (gauze No. 12). All nineteen samples of a pump series were taken on the same day, and each 200 l sample was placed in water from its own depth and carried to the laboratory to be examined and counted. At the same time the temperatures (and partly also the salinity) for each metre were measured. —The method proved to be very suitable, and in contradistinction to earlier experience of plankton-pumping only a very slight percentage of the bottom animal larvae had been hurt. Most of the animals secured in this way thrived even better in the laboratory than those obtained by the net-hauls. The first pump series was carried out on $^{27}/_{7}$ 1937. As the water was pumped up by hand-power, four zoologists had to work from 7 a.m. to late in the evening merely to secure the samples, which could not, therefore, be examined until the next day. In order to

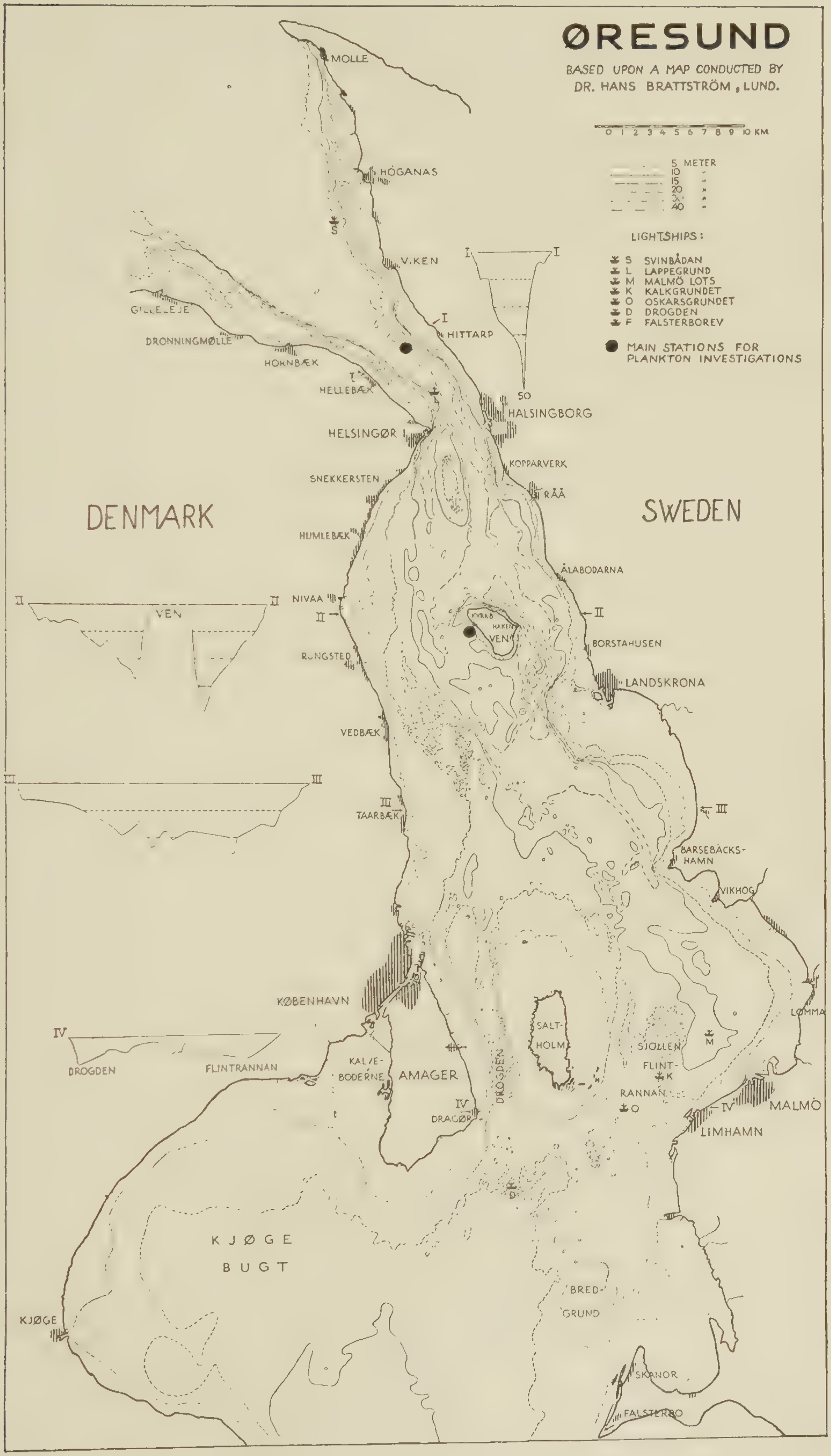

ØRESUND
BASED UPON A MAP CONDUCTED BY
DR. HANS BRATTSTRÖM, LUND.
0 1 2 3 4 5 6 7 8 9 10 KM
5 METER
10
15
20
30
40
LIGHTSHIPS:
S SVINBÅDAN
L LAPPEGRUND
M MALMÖ LOTS
K KALKGRUNDET
O OSKARSGRUNDET
D DROGDEN
F FALSTERBOREV
MAIN STATIONS FOR PLANKTON INVESTIGATIONS
MOLLE
HÖGANÄS
V.KEN
HITTARP
GILLELEJE
DRONNINGMØLLE
HORNBÆK
HELLEBÆK
HALSINGBORG
HELSINGØR
SNEKKERSTEN
KOPPARVERK
RÅÅ
DENMARK
SWEDEN
HUMLEBÆK
ÅLABODARNA
NIVAA
KYRKB
HAKEN
VEN
BORSTAHUSEN
RUNGSTED
LANDSKRONA
VEDBÆK
TAARBÆK
BARSEBÄCKSHAMN
VIKHOG
KØBENHAVN
LOMMA
SALTHOLM
SJOLLEN
FLINTRANNAN
KALVEBODERNE
AMAGER
DROGDEN
DRAGØR
MALMÖ
LIMHAMN
FLINTRANNAN
KJØGE BUGT
KJØGE
BREDGRUND
SKANOR
FALSTERBO
I
II
III
IV
SO

Fig. 2. Chart of the Sound (Øresund) showing the two main-stations for plankton investigations.

avoid this in future series, it was decided to pump up only 100 l from each metre, as the 200 l samples had proved to be extremely rich in animals. Such 100 l series were taken on $^{12}/_{8}$, $^{22}/_{8}$, and $^{25}/_{9}$ 1937, and on $^{30}/_{7}$ 1938. It proved impossible, however, to continue the pump series during the winter season. Our primitive equipment could not withstand the winter storms, and we could not afford the time and number of scientists required for taking such pump series; they were therefore given up for the winter, to be continued next summer. It was evident, however, that the pump series, when carried out from a solid motorboat with a motor-driven pump, would yield much better and more exact results than the more primitive net-hauls, and as soon as possible we intend to continue these pump series with a better equipment and under more favourable conditions. See, however, the discussion and remarks on pump series on pp. 381—392.

C. The rearing methods. The numerous methods of identifying larval stages of marine invertebrates employed by scientists during the last hundred years can be classified into two main categories:

a. Developing eggs of an identified species are obtained either from spawn taken in the sea, from animals which have spawned in captivity, or from artificially fertilised eggs, and are reared to young bottom stages or at least to a larval stage which is sufficiently distinct to be recognised and found again in the plankton.

b. Late-stage larvae obtained from the plankton are partly traced back to younger planktonic stages and partly reared in glass dishes, until they have metamorphosed and grown into a bottom stage characteristic enough to be identified.

During the last decades "method a" has been used with great success by Mortensen (1913, 1920, 1921, 1931, 1937 and 1938) for Echinoderms and by the staff of the Plymouth laboratory (Lebour 1937 a, 1933 c, 1944, Wilson 1932 a, b, 1933, Rees & Russell 1937). Using plunger-jars, and feeding with cultures of *Nitzschia* and other small algae the latter authors have obtained astonishing results for Prosobranchs, Lamellibranchs, Crustaceans, Polychaetes, and Coelenterates. It is no doubt by this method that the best results have been obtained so far, but in order to be really successful such cultures have to be controlled very often. However, this requires a continuous working time of several months, or a laboratory with a permanent staff. Since no such collective working time was at our disposal, and furthermore electric light was installed in Ven as late as 1939, and there is no running water, it has been impossible to use this method there. And during the years at Helsingor we have also been unable to afford the time necessary for using these suitable methods. The second method — b — has likewise been used by several scientists with good results. Especially the results obtained by Stafford (1912) and Kändler (1926) in rearing Lamellibranch larvae in Canada and Heligoland respectively should be mentioned. The best results are obtained, when late-stage larvae nearly ready to metamorphose (such late-stage larvae will normally swim near the bottom of the glass dishes, while younger larvae will swim near the surface) are placed in glass dishes of 2 to 3 dl, with sea-water of a suitable salinity: it has proved very practical, then, to add some thoroughly cleaned pieces of *Ulva* and *Enteromorpha* for aëration. Feeding with *Nitzschia* and *Chlorella* will sometimes further promote the rearing. In this way Opisthobranchs (*Philine, Limapontia, Embletonia*), Prosobranchs (*Littorina, Rissoa, Nassa*), Polychaetes (*Phyllodoce, Harmothoë, Polydora, Lanice*), and Echinoderms (*Asterias, Echinocyamus, Amphiura*) can be reared to young bottom stages (own experience) and thus be identified. This procedure has been very much used during our investigations.

Another method used was the following: Large numbers of vertical plankton samples taken immediately after each other at our fixed station were placed in groups of five samples in aërated 10 l aquaria arranged side by side in a light, but not sunny place. Some of the aquaria contained surface water, others 10 m water, and others again bottom water (from a depth of 18 m). A group of samples similar to those in the aquaria and caught with them was examined, and its content of larvae counted and noted down. In such a series other species of larvae will develop and metamorphose in surface water than in 10 m water or in bottom water, according to their affinity to the water layer in question, and much interesting information was secured in this way. Series of such experiments were carried out on Ven and at Frederikshavn in 1939, and gave very good and interesting results.

To secure young bottom stages for comparison with animals which have metamorphosed in the aquaria, mud was collected by means of a Dr. MORTENSEN's detritus-collector (MORTENSEN 1925). If placed in bottom water in large enamel dishes and examined with a lense after sedimentation, such detritus-samples proved to be very rich in animals. Besides large numbers of *Ostracoda*, *Harpacticida*, *Turbellaria*, and *Nemertini*, very young bottom stages e. g. of *Psolus phantapus*, *Harmothoë imbricata*, *Pholoë minuta*, and of different *Tectibranchiata* were found in this way, but tiny as they are they can only with difficulty be distinguished in the mud, and this method requires much time and great patience.

In spite of many successful results obtained by the methods mentioned above, it is, however, a fact that they failed partially or totally for a large number of species. Even when the plunger-jar method with algal cultures is used, the rearing of several species of larvae proved to be in vain. Thus WILSON (1936a) has made several attempts to rear the larvae of *Nephthys hombergi* and *Pectinaria koreni* without success; NOLTE (1937, p. 57) mentions the total impossibility of rearing the larvae of Maldanids, and LEBOUR (1932, 1933a, b, 1935a, 1936 and 1938a) has had similar disappointing experiences with the larvae of e. g. *Ensis siliqua*, *Saxicava arctica*, *Odostomia eulimoides*, *Stylifer stylifer*, *Eulima alba*, *Philbertia gracilis*, *Turritella communis*, *Aporrhais pes pelecani*, etc.—Many factors may contribute to this, e. g. abnormal food conditions, the temperature, the salinity, the content of Cu (PRYTHERCH 1931, 1934a, b), the growth of Protozoans in the culture dishes, or the want of a suitable substratum for the metamorphosis. In a series of very fine experiments DAY & WILSON (1934), and WILSON (1932b, 1937) have shown that Polychaete larvae of the genera *Scolecolepis*, *Notomastus*, and *Owenia* will metamorphose much earlier when the substratum in the culture dishes is suitable, and MORTENSEN (1921) mentions similar experiences of metamorphosing larvae of Echinoderms. Recently, JÄGERSTEN (1940) has studied these problems in the Archiannelid *Protodrilus rubropharyngeus*. He found that the mechanical character of a substratum was insufficient to induce the metamorphosis of the larvae; an inorganic, unknown substance associated with a substratum was necessary in order to induce the larvae to metamorphose. Larvae which could easily be made to metamorphose in shell-sand from the littoral zone were quite negative in shell-sand (*Amphioxus*-sand) from depths of 20 m. The experiences of ALLEN (1914) and HARVEY (1939) on the growth of the diatoms *Thalassiosira gravida* and *Ditylum brightwelli* respectively, viz. that two organic substances or groups of substances are required for a vigorous growth of these species in artificial sea water, seem to point in a similar direction. A continued examination of these problems will no doubt show a very intricate group of processes, which we are at present unable to understand, and which, together with the other facts pointed out above, will also in the future make rearing of larvae in captivity a very difficult problem.

D. Cages in the sea. Our intention, as soon as possible to rear and identify planktonic larvae of all bottom invertebrates in Danish waters, forced us to find out other methods than those hitherto used. The most effective procedure would, of course, be to rear the larvae in "cages" in the sea. Nolte (1937, p. 63—64) has already proposed this method for Polychaete larvae, but as far as can be seen from his paper, he has had no opportunity of realising his plan. Smith (1935) tried to rear *Patella vulgata* larvae in culture dishes, but found that the best results were obtained when jars covered with plankton gauze were immersed in tanks with running sea-water.—On Ven the following procedure was adopted: Small "cages" were constructed, consisting of two ordinary medicine bottles cut across at the middle. One bottle with the neck upwards and another with the neck downwards were connected by a cylinder of plankton gauze coarse enough to allow small food particles (Flagellates, Diatoms, etc.) to pass through and fine enough to retain the larvae placed inside (cf. fig. 3). The lowest bottle was corked, filled with sea-water taken from the depth at which the cage was to be placed, and a sterile substratum (mud, sand, shells, or a mixture of these) was placed in a layer 2 to 3 mm thick upon the cork in the lower bottle-neck. Then, old larvae of the species desired were separated from fresh plankton samples and 20 to 50 larvae were pipetted down into the lower bottle in each cage, which was then as quickly as possible (to avoid increasing temperatures and other abnormal conditions) transferred to the sea to the depth chosen and kept there for a longer or shorter time.

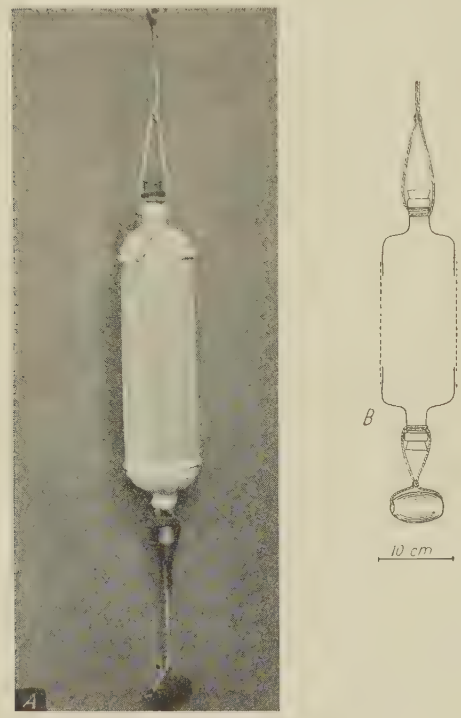


Fig. 3 A-B. "Cages" of plankton gauze for rearing of pelagic larvae in the sea. — *A*. "Cage" ready for use. — *B*. A similar "cage" in longitudinal section.

On $^{6-8}/_{8}$ 1938 a series of cages with fairly old larvae, among others of the genera *Acera, Retusa, Alvania, Aporrhais, Saxicava, Lima, Montacuta,* and *Polydora,* were placed at a depth of 16 m at our fixed station off Ven. When hauled in and examined on $^{27}/_{8}$, the results proved to be very poor. Only one specimen of *Saxicava* had metamorphosed, one specimen of *Retusa* was still alive but had not grown at all, and the rest, including all the other genera, had died! They were found dead and in dissolution and without having metamorphosed in the substratum in the bottle-neck. — This mishap may presumably be ascribed to the rather brackish surface layer which the cages had to pass through and to the rather variable salinity and temperature during the period in question even at a depth of 16 m. While the free-swimming larvae have a chance of moving in accordance with the water masses and thus can always choose the conditions they prefer, larvae in a cage are compelled to endure the conditions prevailing there, and will die if these conditions are too unfavourable for them. This method, therefore, proved unpractical for investigations in the Sound (at least off Ven), and was discontinued for the time being. However, when I describe this unsuccessful attempt at such length here, it is because I am convinced that the method in question will prove successful and valuable in localities in which the temperature and salinity are more uniform throughout the whole water-mass (in Danish waters e. g. in the Isefjord and in the Limfjord). Technically the cages seem to function very well, they are cheap in production, easy to handle, and at least 20 per cent of the larvae placed in them were found again (dead and partly dissolved) in spite of their small size, when the cages were re-examined after having been exposed for about three weeks.

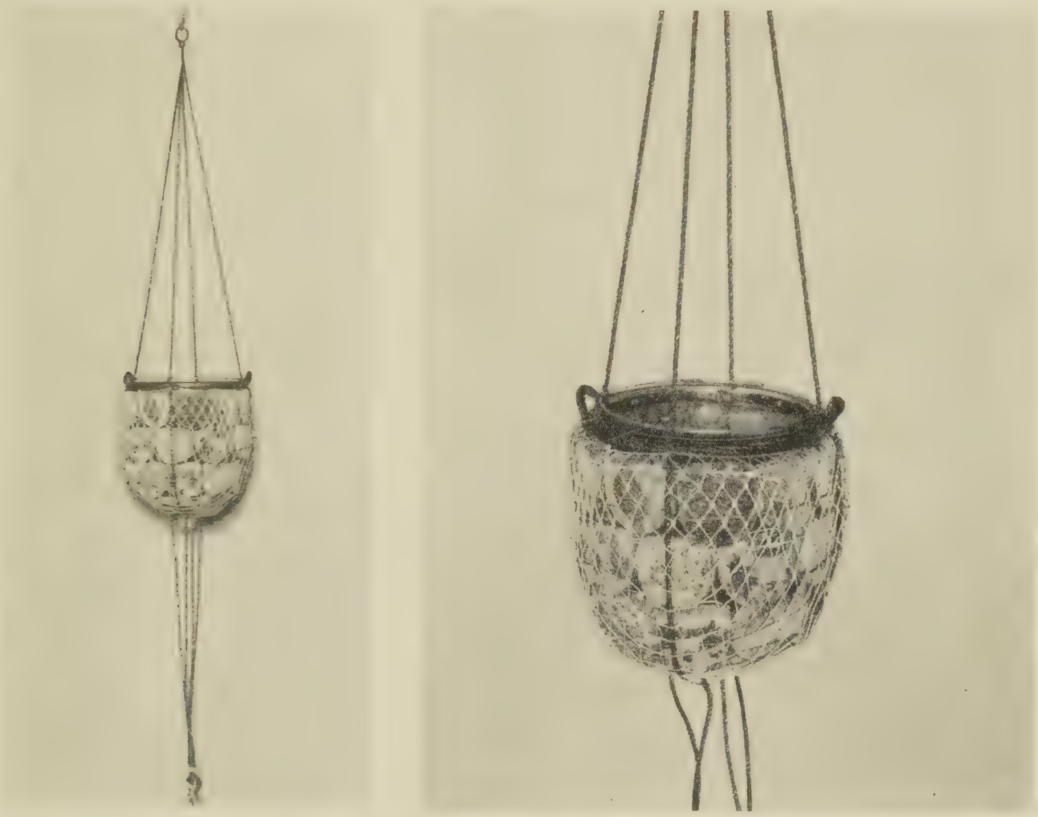


Fig. 4 A-B. The bottle-collector (see the explanation on pp. 19—23).

However, in spite of the mishap the cage experiments gave quite unexpected and most valuable results, for after 3 weeks in the sea the cages contained young living bottom stages of several forms, the larvae of which had not been placed in the cages to metamorphose, and which, therefore, must have entered the cage from the sea as young larvae and completed their development in the cage. Thus, *Mytilus, Capitella, Amphiura* and several other young bottom stages were found living in the substratum in the bottle-neck. This discovery led to the construction of an apparatus which after several experiments and improvements has turned out to be of the greatest value for our continued investigations, namely:

E. The bottle-collector (figs. 4 and 5). The construction is quite simple. A large bottle without a bottom, placed with the neck downwards, is covered externally with a thick layer of cork, light enough to keep the bottle afloat. From the bottle-neck downwards and from the opposite part of the bottle upwards pass 4 lines joining each other in a thimble about $1\frac{1}{2}$ m from the bottle. When a cork has been put in the bottle-neck (and firmly tied there) the bottle-collector will be ready for use. A heavy stone is fastened with a coir rope to the lower thimble and another coir rope provided with a cork float and a slender wooden float is attached to the upper thimble. The bottle-collector will be dragged towards the bottom by the heavy anchoring-stone, while the cork around the bottle will carry it upwards until the lines between the stone and the bottle are taut, and the bottle will remain in this position as long as it remains in the water. To avoid disturbance and rolling of the bottle in rough weather the rope between the bottle and the surface is provided with a cork-float 1—2 m below the surface of the water (fig. 5), and from this float the rope continues to the surface, ending there in a slender wooden float, which makes the least possible resistance to the currents. By lengthening and shortening the anchor rope the bottle-collector can be placed at any depth desired, or several collectors can be placed above each other. In our experiments the collectors have hitherto been placed at a depth of 16 m, i. e., just above the bottom at our fixed plankton station (bottom-depth 18 m), and here the individual collector was normally left for about 6 weeks before being hauled in and examined, which in calm weather may be easily done by two men in a jolly-boat. On arrival at the laboratory, the collector, which still contains nearly the same water mass as in the sea, is placed in a rack and aërated like an aquarium. Here the animals will thrive well for several days and can be pipetted up and examined by and by. Of course the young animals sitting on and in the cork-pieces (see below) have to be examined first.

Large numbers of young animals ranging from late larval stages to metamorphosed bottom stages were found in these collectors, which surpassed even our most sanguine expectations. If a piece of wood (for *Teredo, Limnoria* etc.) and some empty mollusc shells or pieces of limestone (for *Polydora, Dodecaceria, Cliona* etc.) are added, the collector would seem to contain nearly all substrata used by the bottom animals—except sand. *Mytilus* and *Mya* settled on the coir ropes (*Mytilus* to a number of $^1/_4$ to $^1/_2$ million of young per rope), *Balanus* and *Pomatoceros* on the cork float and the cork layer, young metamorphosing stages of *Zirphaea crispata* had commenced to bore in the cork layer, where also young *Nassa, Rissoa, Hydrobia,* and *Littorina* (together with young algae) were numerous. On the steep clean glass walls inside the collector Serpulids, Balanids, Hydroids, and *Anomia* settled, often in very large numbers; on the oblique glass flats between the steep cylindrical walls and the bottle-neck were found the young of tube-building Polychaetes, *Corophium* and Chironomids and other forms, which without living directly in the clay bottom use particles of detritus for fortifying their tubes. Finally, the layer of detritus in the bottle-neck was teeming with the young of invertebrates associated with really soft bottom.—It is unnecessary to add sterilised mud or other soft substrata, as the depositing detritus will very soon form a layer in the bottle-neck sufficiently thick to protect and conceal the young. It seems very difficult, however, to obtain a pure sandy substratum in the collectors, as it will soon be overlain by depositing detritus. To avoid this, I would propose putting the collector in a place with a strong current and making the bottle less deep (i. e. less stagnant water and therefore less sedimentation of detritus above the sand), but so far this has not been tried in practice.

Summarising the facts given above, the following advantages can be pointed out for the bottle-collector:

A. It is cheap to procure and can be handled by two men from an ordinary jolly-boat.
B. When placed in a suitable locality, it can be left without control for months.

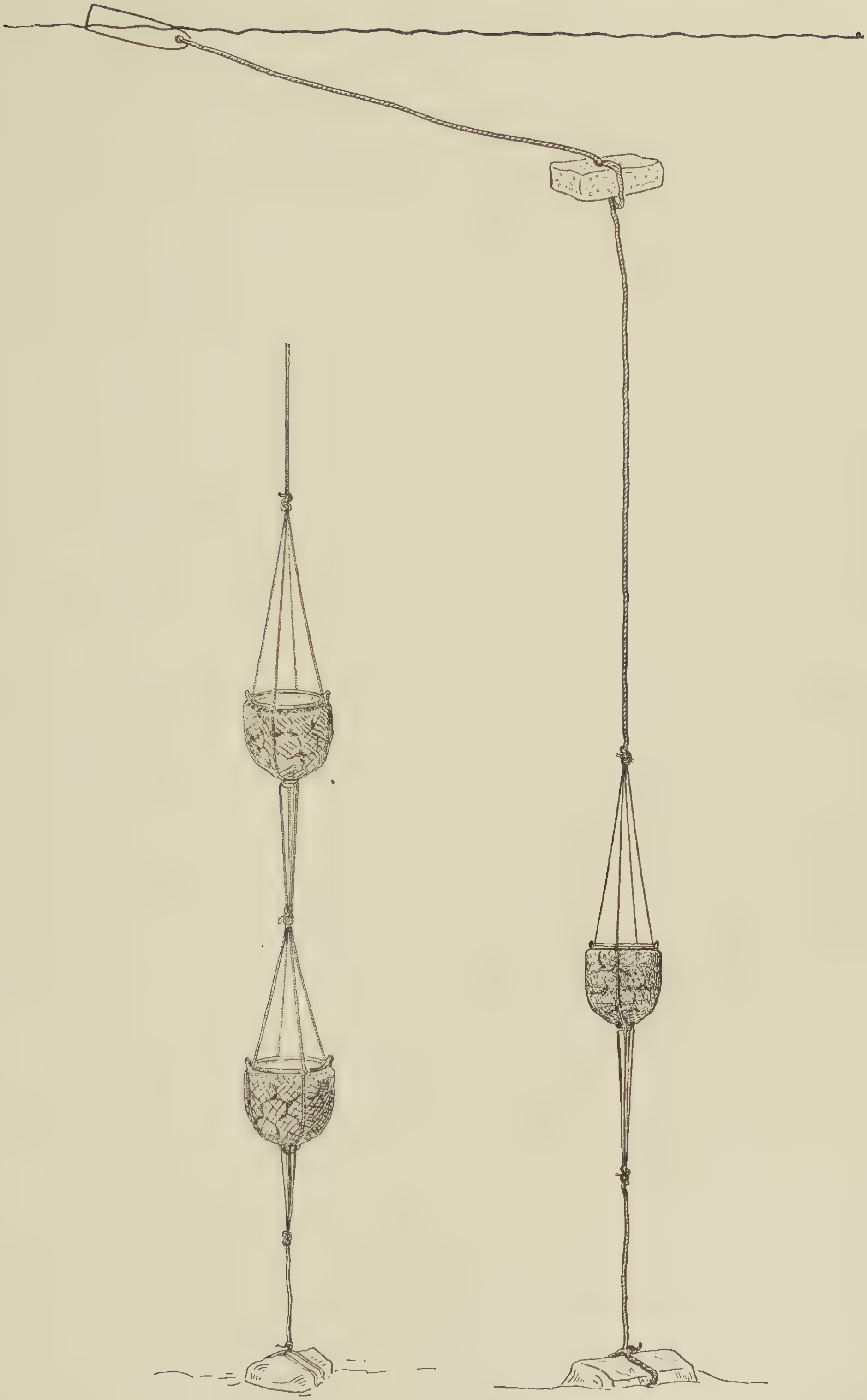


Fig. 5 A-B. Bottle-collectors placed in the sea. To the right a single bottle-collector »in situ« with its anchor stone, with the cork-float 1—2 m below the surface, and with a slender wooden float at the surface. To the left a sketch showing two bottle-collectors attached to the same rope but at different distances from the bottom. (Drawn by POUL H. WINTHER).

C. As it includes all substrata of importance to bottom invertebrates with the exception of sand, it will collect a very high percentage of the species of metamorphosing larvae which leave the plankton in the area in question.

D. When hauled up with care, the water mass contained in the immersed bottle-collector will pass the surface layer nearly quite intact, and the animals inside can be transferred to the laboratory under nearly natural conditions.

E. Since the collector may serve as an aquarium in the laboratory, the animals secured can remain "in situ" until examination and will thrive better and live longer than animals derived in other ways and later placed in aquaria.

F. All stages of soft bottom animals collected will crowd into a small portion of detritus in the bottle-neck and can easily be found and separated. (To look for young bottom stages on a large scale in a sample of mud derived from the sea-bottom itself is an almost hopeless task. The tiny young are extremely well hidden, and to find only a few of them large quantities of bottom-material must be examined. Wilson (1937), therefore, rearing Polychaete larvae in dishes with muddy or sandy substrata, used funnels as aquaria, because all settling larvae would then crowd into a few c.cm of substratum in the narrow part of the funnel and could then easily be recognised. The same principle is used in the bottle-collector.)

Fig. 4 A-B shows the bottle-collector in detail. Large exsiccator-bottles, which are very strong and are strengthened along the brim, are best suited for the purpose. Covered externally with a cork layer, such bottles will prove very resistant. It is necessary to tie the cork onto the bottle-neck since otherwise the heavy water pressure, when the collector is hauled up, will force out the cork. Experience has shown that to give sufficient results the collector must remain for at least six weeks in the sea, probably because the collector has to be covered with a crust of Diatoms and to be provided i. a. with the "substance" mentioned by Jägersten (1940) as promoting metamorphosis, before it will function as a natural substratum.

A bottle-collector exposed in a water area in which large numbers of floating algae will attach themselves to the suspended coir rope will often, when hauled up, catch some tufts of algae from the rope above. These algae with their epifauna will confuse the picture of the young which have really settled in the collectors, and will make a thorough examination of the contents of the collector troublesome and difficult. This inconvenience may be avoided by placing a protecting cover on the rope some 2—3 m above the collector, which will stop the algae and prevent them from reaching the collector. A still better method is to place a 1 m high cylinder of coarse-meshed stramin over the mouth of the collector in the same way as the cylinder of plankton gauze is placed in the cages shown in fig. 3 A-B. Our experiences have shown that larvae will enter these cylinders in great numbers. The coarse meshes will allow larvae as well as phytoplankton to pass through, while larger enemies and floating tufts of algae will be excluded. The results obtained have shown that under certain conditions this construction will yield still better results than bottle-collectors without such a cylinder. It must, however, be borne in mind that after a stay in the water of about six weeks the stramin-gauze will decay and break. Hence, a new cylinder must be used for each single exposure of the collector.

During the summer and autumn of the years 1939—42 young bottom stages of about 70 different invertebrates were secured by means of the bottle collector, and this only from one single locality and from a depth of 16 m. Similar bottle-collectors used in the Copenhagen harbour by mag. sc. Erik Smidt in the summer of 1940 have added several species to this number. Among the young bottom stages collected in this way the following deserve special mention: *Phoronis mülleri*, the bottom stage of which has never before been recorded from Danish waters, but which proved to settle normally in our bottles both in 1939 and in 1940. *Porcellana longicornis*, common in northern Kattegat but never found in the Sound, settled in a bottle-collector in August 1939, and *Chaetopterus variopedatus*, which is only known from occasional adults from the Sound, and the larvae of which have never been taken in our main series off Ven, was a common inhabitant of our bottle-collectors there during the summer of 1939.—No doubt the coming years will add several species to those mentioned above, and bottle-collectors will be used in our investigations to an increasing extent.

III. The Area investigated, its Topography and Hydrography (cfr. the chart fig. 2).

The Sound has no distinct boundaries towards the surrounding seas. To the north it merges into the Kattegat, to the south into the Baltic. The chief limit within the area: Kattegat—the Sound—the Baltic is found in the Sound itself by the threshold between Amager and Limhamn. The limits normally applied to the area in question are: Gilleleje—Kullen in the north, and Stevns—Falsterbo in the south, i. e. an area of 2400 sq.km (acc. to the Royal Danish Hydrographic Office). The 1100 sq.km fall upon the area south of the threshold Amager—Limhamn, an area which from an ecological point of view must be referred to the Baltic, and which is of little importance in the present investigation. The area of 1300 sq.km north of the ridge consists of two ecologically distinct provinces, viz. the area: Amager—Taarbæk—Barsebäckshamn—Limhamn, 500 sq.km, where unmixed salt Kattegat-water is normally absent from the bottom, and the area: Taarbæk—Gilleleje—Kullen—Barsebäckshamn, 800 sq.km, in size, with a salt Kattegat-layer along the bottom below the Baltic surface layer. Both our main stations are situated within this latter area, which by the narrow passage of barely more than 4 km between Helsingør—Hälsingborg is divided into two smaller areas. In this paper the area from Helsingør—Hälsingborg northwards will be designated "the northern part of the Sound", and the area south of Helsingør—Hälsingborg with Ven as a centre will be designated "the middle part of the Sound".

As mentioned above, between Amager and Limhamn a threshold occurs only 7—8 m below the surface, which divides the Sound into two very distinct areas: a rather shallow area with depths from 0—15 m (20 m) in the south, and a northern area with much greater depths, which towards the north passes evenly into southern Kattegat. This northern area comprises the last outposts of a deep channel, which — about 40 m deep — follows the Swedish west coast from Bohuslän southwards. The main part of the bottom north of Helsingør is, thus, situated at depths of 20—40 m, and this deep area continues southwards east of Ven down to Barsebäckshamn (average depth 20—30 m). The bottom west of Ven presents depths of 18—20 m, decreasing towards the Danish coast, and a still more shallow-watered area (down to 15 m) is found between Taarbæk—Barsebäckshamn in the north and Amager—Limhamn in the south.

The water masses of the Sound are composed of two distinct layers.

The surface layer (the Baltic water layer) flows from the Baltic northwards to the Kattegat, and has a low salinity, viz. at the surface 11—14 $^0/_{00}$, at a depth of 10 m 12—22 $^0/_{00}$. The salinity is lower in the summer than in the winter. The maximum temperatures are found in August, viz. 16.5° to 17° C at the surface and 15.5° to 16.5° C at a depth of 10 m.

The minimum temperatures are reached in February—March, viz. 0° C (or even negative temperatures) to 1.9° C at the surface and 1.9°—3.3° C at depths of 10 m. The rise in temperature is greatest from April (3.5°—4.5° C at the surface) to June (12.5°—13.5° C).

The bottom layer (the Kattegat layer) flows from the Kattegat southwards into the Sound, and has a higher salinity, viz. at a depth of 20 m about 32 $^{0}/_{00}$, at depths exceeding 30 m: 32—34 $^{0}/_{00}$ (the salinity at these depths in the Sound is thus just as high as at the corresponding depths at Læsø Trindel). At a depth of 20 m the maximum temperature, viz. 12.6° C, is reached in September, the minimum, viz. 4.7° C, in March. At a depth of 25—30 m the maximum temperature, viz. 10—11° C, is found in September to November, the minimum, viz. 4—5° C, in March to May. At greater depths than 30 m the maximum temperature, 10.5° C, is reached as late as November, the minimum, 4.3° C, in May. The rise in temperature is greatest from June (7°) to August (11°) at a depth of 20 m occurring later and later in the year as the depth increases.

The brackish Baltic water layer—the only water mass present south of the threshold —north of the threshold forms a north-moving surface stream overlaying the salter, south-going Kattegat water. These two water layers may vary in thickness in different places and different months. The Baltic layer has an average thickness of from 8 m (Steemann Nielsen 1940, p. 33) to 15 m (Brattström 1941, p. 102) (cf. also this paper p. 381, table). Experience seems to show a somewhat smaller thickness off Ven than in the northernmost, deepest part of the Sound. Conditions like those outlined here will normally occur in the Sound during two-thirds of the year. During one-third of the year south-going water or—very rarely—stagnant water will be found at the surface (Steemann Nielsen 1940, p. 35, Brattström 1941, p. 73—74). South-flowing water at the surface of the Sound will, however, often mean that Baltic water, which has reached the surface of the Kattegat, will be forced back into the Sound by a westerly gale, i. e., even when the current moves southward, Baltic water more or less mixed with Kattegat water will often dominate at the surface. During short periods with a maximum salinity in the Sound a salinity of up to 25 $^{0}/_{00}$ has been ascertained at a depth of 10 m off Amager (Brattström 1941, p. 86), but it may be taken for granted that Baltic water will constitute the dominating element of the surface layer in the Sound during more than three-fourth of the year. And this Baltic layer is often very quickly renewed. Steemann Nielsen (l. c., p. 33) is of opinion that the whole surface layer of the Sound during a constant period with north-going surface currents is renewed in less than three days.

While the Baltic water layer uses the Sound as a route of passage from the Baltic to the Kattegat and the North Sea, the Kattegat water, which enters the Sound from the north, is stopped by the threshold between Amager and Limhamn. This means that the area in question functions as a "sound" in so far as the Baltic water layer is concerned but as a "fjord" in the case of the Kattegat layer. Already in the area between Taarbæk—Barsebäckshamn and this threshold a portion of the saline bottom layer will be forced towards the surface to be mixed with the lower part of the Baltic water and carried northward with this. The Kattegat water thus removed is replaced by new quantities of Kattegat water entering the Sound along the bottom. This renewal of the Kattegat water is, therefore, mainly kept up by the Baltic current. Thus, the north-going surface layer comprises not only Baltic water but also part of the Kattegat water, i. e. it comprises a much larger volume of water than that of the south-going bottom layer. Accordingly the north-going surface current is stronger in the northern than in the southern part of the Sound (Jacobsen 1925, p. 56; Brattström 1941, p. 75), and normally much stronger than in the bottom layer.

The spring layer is usually so distinct that a simple measurement of the temperature from every metre throughout the water column will clearly show its situation. During other periods of the year the spring layer may, however, be totally absent (cf. e. g. the table from Ven on p. 381, where a spring layer is absent during January, March, April, October, and November). As regards the relations between salinity and bottom invertebrates in the Sound, it will suffice to refer here to the conclusion arrived at by Brattström (1941, p. 103), viz. that the combination: high salinity — sandy bottom — vegetation, as well as the combination: low salinity — clayey or muddy bottom — no vegetation, are both of them rare in the Sound.

For further topographical and hydrographical details the reader is referred to the authors cited above, especially to the paper of Brattström (1941), who has collected all data which are of essential importance for the biological conditions in the Sound.

IV. Synopsis of Reproduction and Larval Development.

During the working up of the main series from the four years' investigations in the Sound, all larvae of bottom animals have been counted and referred to their systematic group. Owing to the present conditions, however, these systematic groups have not all of them been studied in equal detail. The main study has been focussed on the four large groups: *Echinodermata*, *Polychaeta*, *Gastropoda*, and *Lamellibranchiata*, which together constitute the absolutely dominating element among the planktonic bottom animal larvae. A single group of Gastropods – the *Nudibranchiata* – has, however, larvae which are so similar mutually and so difficult to distinguish from each other when met with in the plankton that their identification must be referred to a special, detailed study. Here they are only dealt with rather summarily. — The same is the case with the larvae of the *Nemertini*, and the *Anthozoa*, which are also difficult to identify and which are furthermore of no importance in the plankton. The larvae of the *Bryozoa* (the *Membranipora*-group) and the *Phoronidea* have been studied in somewhat more detail, though not on the same scale as the large groups mentioned above. — Among the *Crustacea*, larval Balanids with their varying stages and sizes within the individual species have only been treated summarily, while larval *Decapoda* have been identified and counted separately. As to this latter group it seems, however, that our standard nets, so suitable for collecting most other larvae, are too small to secure a sufficiently large number of these rapidly swimming larvae to enable us to give a reliable account of their number of species and specimens at the different seasons. – The larvae of *Spongia*, finally, do not seem to occur in our main series. Most probably they are so small that they will normally escape through the meshes of the nets, and as their pelagic life is very short, they are of no significance at all in the plankton. They have not been dealt with here. As regards reproduction the *Hydrozoa* may in the main be regarded as pelagic animals, not as bottom invertebrates. Their larvae are of no importance at all in the plankton, and — like the Sponges — they have been disregarded in the present survey.

The aim of this synopsis is to serve as a provisional handbook on the reproduction and pelagic larvae of Danish marine invertebrates. Hence all the available literature has been used and briefly summarised and referred to for each single species, while fresh experience from Danish seas is added under the term "Own remarks". Not only the pelagic larval development, but also all data for species with a non-pelagic development have been considered. The survey especially comprises the fauna living in the Sound within the limits Gilleleje—Kullen in the north and Amager—Limhamn in the south. All species from the literature, those added through our own collections, and such as are only known as "drift-larvae" carried to the Sound with currents from the neighbouring areas, are contained in the lists, which, thus, for certain groups furnish several new additions to the fauna. A brief note after the name gives — for the larger groups – the distribution and frequency of the adult species within the area investigated. Species which live in Danish waters outside the Sound, and on which fresh observations of the reproduction are available, are likewise included (in brackets) in this synopsis. – Cf. also the preliminary remarks given in the synopsis for each single group. – The figures have been drawn by the author, those of Lamellibranch larvae by Mr. C. BARKER JØRGENSEN. An index to the synopsis is given at the end of this paper.

1. Anthozoa.

Larvae of *Anthozoa* are of no importance at all in the plankton of the Sound. They are rather difficult to recognise, several species being so similar to each other that it is impossible to identify them on the basis of our present knowledge, and since, moreover, several of the larvae are very small, occasional specimens have probably often been overlooked in our main series. – The study of the reproduction of this group must therefore be based upon careful observations of each single species in the aquaria — an investigation for which we have hitherto been unable to spare the sufficient time. A detailed study of the reproduction of *Anthozoa* in the Sound must therefore be postponed to some future time; here only the rough outlines will be briefly discussed.

Working up this chapter, I have had the opportunity to use the complete manuscript on the *Anthozoa*, now (1945) published in the "Danmarks Fauna", prepared by Professor O. CARLGREN, Lund, who gives i. a. a list of all the *Anthozoa* known from the Sound, viz. the following 16 species:

Alcyonaria: Virgularia mirabilis and *Alcyonium digitatum*. According to FR. J. MADSEN (1943), the record on *Pennatula phosphorea* from the water off Hellebæk does not seem to be correct, but recently Dr. BRATTSTRÖM, Lund, has told me that he has seen a specimen of it from the Sound.

Ceriantharia: Cerianthus lloydii.

Athenaria: Edwardsia longicornis, Edw. danica, and *Halcampa duodecemcirrata.*

Thenaria: Bolocera tuediae, Tealia felina coriacea, Stomphia coccinea, Hormathia digitata, Sagartia troglodytes, S. elegans, Sagartieton laceratus, S. undatum, and *Metridium senile dianthus.*

The reproduction of the northern *Anthozoa* is still very poorly known, and it has hitherto been quite impossible to recognise and identify most of the larvae in the plankton. To show our present knowledge, and to give the lines for future work on these problems, I think it reasonable to briefly summarise what is known at present about the reproduction of each single species living in the Sound.

Alcyonaria.

Alcyonium digitatum LINNÉ. Studied by MATTHEWS (1913, 1917), and HICKSON (1901). Male and female colonies spawned in the Plymouth aquaria on $^{27}/_{1}$ to $^{3}/_{2}$-1912. The ripe, reddish-brown eggs are 500 μ across. "Each ovum takes at least ten minutes to pass through the stomodæum". Fertilisation outside the mother, where the floating egg develops into "a round, ciliated planula", which is later transformed into "an oval swimming planula" of a pale yellowish colour. Later, again, the larva assumes a pear-like shape, "swimming with the broad anterior pole forward, and simultaneously rotating on its axis". The planula is hollow and provided with a layer of equally long cilia over the whole surface (Hickson 1901, fig. 18). Larvae spawned between $^{27}/_{1}$ and $^{3}/_{2}$ had already settled on the glass walls near the surface on $^{6}/_{2}$, but no tentacles developed until $^{17}/_{2}$. The larvae take no food from the plankton, i. e. they are lecithotrophic (cf. this paper pp. 436—438).

Virgularia mirabilis O. F. Müller. Grant's (1829) and Dalyell's papers (1839, pp. 188—189, with a figure of the larva pl. 18, fig. 11, and 1848) are not available in this country, but Jungersen (1888 and 1904) and Sten Berg (1941) summarise and discuss the results attained by Dalyell, from which the following facts may be quoted: Breeding near the British Isles in April-May-June. Egg-size not mentioned. The eggs spawned develop in the course of two days into free-swimming larvae of the typical planula shape (Dalyell has introduced the term "planula" in zoology). Dalyell, however, observed no ciliation, which tends to show that the cilia were small and equally distributed all over the body without any ciliary tuft at the aboral pole, i. e. a type like that known for *Alcyonium*. — A week later the larvae settled on the bottom, and subsequently the tentacles developed.

Pennatula phosphorea Linné. Nordgaard (1912) observed the spawning of reddish-yellow eggs floating in the water in aquaria at Bergen in October 1889 and 1901. This seems to agree well with the type known for *Alcyonium*, while the larvae, though observed by Dalyell (1848), are not described. Aurivillius (1898 a) found ripe sperm and eggs at Kristineberg in November.

Discussion of the Reproduction in *Alcyonaria*.

The few records on the reproduction of northern *Alcyonaria* seem to indicate that they spawn large reddish-yellow eggs rich in yolk, which float in the water and there develop into actively swimming planulae with a uniform ciliation all over the body. The planulae are lecithotrophic (cf. pp. 436—438), and a few days or a week after fertilisation they will settle on the bottom. The tentacles are formed after the settling. — Larvae of this type may, accordingly, be confused with larvae of *Bolocera*, *Tealia*, or *Stomphia* (cf. these). — It seems likely that some fairly large yellowish-red to colourless Planula-larvae found in our plankton off Ven on $^{12}/_{11}$ 1938 (5 spms.) and off Helsingør on $^{11}/_{11}$ 1941 should be referred to this group, and if so, it seems most reasonable, from their occurrence in November, to refer them to *Alcyonium digitatum*. However, no definite proof can be given.

Ceriantharia.

Cerianthus lloydii Gosse. Nyholm (1943) has studied the development of this species at Kristineberg (Bohuslän). The adults are hermaphroditic. Spawning in winter at 5°—7° C. The newly spawned egg, 230 to 250 μ across, is olive-green in direct light and floats in the water, where the fertilisation takes place. Three days later the first gastrulae are seen; they are ciliated, and swim with the aboral pole forward, rotating on their longitudinal axis. This rotation will cease as soon as the tentacles begin to appear. The tentaculated larvae — the *Synarachnactis bournei* — have a long planktonic life. At first four tentacles develop, but the larva will not leave the plankton until eleven to thirteen tentacles have developed. The larvae feed on phytoplankton and grow fast during the pelagic stage. The older larvae are able to feed on zooplankton also, e. g. on young fishes (Lebour 1922). The four-tentacle-stage is 500 μ, the seven-tentacle-stage about 2000 μ, and the eleven-tentacle-stage 2500 μ. The larvae occur in the Bohuslän-plankton from February to June. — Discussion: The larvae in question differ from most other northern larval *Anthozoa* by their large size, by their tentacles developing already during the larval life, by their considerable growth during the planktonic life, and by taking food from the plankton during their planktonic life. Larvae of this species have only once been met with in the Sound, viz. on $^{17}/_{10}$-1936, off Ven, two specimens with several tentacles resembling those figured by NYHOLM (1943, pl. 6, fig. 12 and text-fig. 10 A). Older stages have hardly been overlooked in our samples.

Athenaria.

Edwardsia longicornis CARLGR. Reproduction and larval stage unknown.

Edwardsia danica CARLGR. Reproduction and larval stage unknown.

Halcampa duodecemcirrata M. SARS. Reproduction and larval stage unknown. NYHOLM (1943, p. 213) states that *Halcampa sp.* is oviparous.

Discussion of the Reproduction in *Athenaria.*

Apart from the observations on *Peachia hastata*, which has tentaculated, not free-swimming, larvae parasitic on various medusae, nothing seems to be known about the reproduction and larval development of the northern Edwardsiids. CARLGREN (1937) states that the larvae of the genus *Halcampa* are not parasitic, and doubts whether parasitic larvae occur at all within the genus *Edwardsia*. WIETRZYKOWSKI (1910, 1914) describes the development of the French species *Edwardsia beautempi*, examined at Roscoff, and since this species has free-swimming pelagic larvae, as is probably the case within most of the northern species also, it seems reasonable to briefly summarise WIETRZYKOWSKI's results; these are as follows: Breeding in September. The eggs, spawned through the mouth, 200 μ across, rather poor in yolk, with a very thin egg-membrane, are fertilised in the water, and the slowly swimming gastrula is formed 48 hours later. The older, planktonic larva is three times as long as broad and has a tuft of long cilia at the aboral pole. Four equally long tentacles are formed before the larva leaves the plankton and settles on the bottom. One of the tentacles appears before the others. The larvae take no food from the plankton, i. e. they are lecithotrophic (cf. pp. 436—438), and in aquaria they may swim about up to one month before settling. — Probably most of the northern species reproduce in a similar way, and if so, the Edwardsiid-larvae are characteristic by the older stages having four tentacles (up to 13 tentacles in *Ceriantharia*) and a tuft of long cilia at the aboral pole (not found in *Ceriantharia*). — Thus it is quite possible that at any rate the older stages of the larval Edwardsiids will be recognised when met with in the plankton.

Thenaria.

Bolocera tuediae (JOHNST.). APPELLÖF (1900, p. 6—7) describes the egg. NYHOLM (1943, p. 212) states that the species is oviparous, and GEMMILL (1921) gives an account of the whole development. The species has separate sexes. Spawning in March (GEMMILL l. c.) to July (STEPHENSON 1929, p. 158). The pink eggs, very rich in yolk, which float in the water, are by far the largest of all Actinian eggs in the Clyde Sea area, viz. about 1100 μ across. The gastrula is formed 6 to 7 days after fertilisation, and 3 to 4 days later the larva attains an oblong shape, swimming with the aboral pole forwards and rotating on its own longitudinal axis. The oldest planktonic larvae are pear-shaped, the aboral end being narrower, and there is no elongated tuft of cilia at the aboral end. "Fixation occurs about twenty-five days after shedding the eggs", and even the older larvae remain on or near the bottom. The pelagic larvae take no food from the plankton, i. e. they are lecithotrophic. The tentacles are not formed until the larva has settled (GEMMILL 1921).

Tealia felina LINNÉ var. **coriacea.** The whole larval development has been described by APPELLÖF (1900). — NORDGAARD (1912), GEMMILL (1920 a, p. 579), STEPHENSON (1935, p. 153), NYHOLM (1943, p. 212), and CARLGREN (1921, p. 162) add supplementary remarks. The following summary is based on these papers: Spawning at W. Norway in February to April. Eggs and sperms are here shed freely in the water, where the fertilisation takes place, i. e. the adults are oviparous. According to NYHOLM (l. c.) they may also be larviparous near Bohuslän, while viviparity — known as the common mode of reproduction in the arctic form *Tealia felina crassicornis* (cf. CARLGREN 1921) — is unknown in the *coriacea*-form in boreal seas (STEPHENSON 1935, p. 153). The eggs spawned are yolky, 600 μ across (700 μ across in the arctic *T. f. crassicornis*), and float in the water, where they develop into ellipsoid Planula-like larvae with equally long cilia around the whole body. No tuft of long cilia at the aboral pole. The larva in question swims about, but takes no food from the water mass, i. e. it is lecithotrophic, and resembles closely that of *Bolocera tuediae*, though it is somewhat smaller. The tentacles do not appear till long after the larva has settled on the bottom.

Stomphia coccinea (O. F. MÜLLER). GOSSE (1860, pp. 223—226) states that the species is oviparous, and that the largest eggs found in the mesenteries are about 750 μ across (= 0.03 inch); the egg-membrane is 70 μ thick. The egg is scarlet-coloured. No observations on viviparity in this species are known. Hence it seems most likely that the eggs spawned will develop in a similar way to those of *Bolocera tuediae* and *Tealia felina coriacea*. Thus the egg size in *Stomphia* (750 μ across) is larger than that of *Tealia f. coriacea* (600 μ across) and even than that of the viviparous *Tealia f. crassicornis* (700 μ across), while the eggs of *Bolocera tuediae* measure 1100 μ across. — It seems therefore reasonable to suppose that the larvae are large, ellipsoid, equally ciliated, and lecithotrophic (cf. pp. 436—438) without any tentacles in the pelagic stage. However, nothing definite can be stated.

Hormathia digitata (O. F. MÜLLER). STEPHENSON (1935, p. 267) records viviparity in this species from England. However, only one single case is known in which two young — one of them with more than 24 tentacles developed — were found in the gastral cavity of the mother animal. This seems to be the only known observation on the reproduction of the species.

Sagartia troglodytes PRICE. Asexual reproduction unknown (STEPHENSON 1929, p. 146; 1935, p. 338). This species, which is a protandric or synchronous hermaphrodite near England (STEPHENSON 1929), near Bohuslän spawns only one type of sexual products per specimen during each breeding season (NYHOLM 1943, p. 167), and two or more specimens crowd together to spawn, thus fertilising each other (l. c., p. 172—173). The species is oviparous near Bohuslän (eggs 80—90 μ across, NYHOLM 1943, pp. 169, 175, and 213), but normally it is larviparous near the British Isles (STEPHENSON 1935, p. 338) and in the North Atlantic (CARLGREN 1942,

p. 8); there may be produced "over 60 young in a night by two small specimens" (Dalyell 1848). The species may also be viviparous, with young hatching in the crawling stage (Stephenson 1929, p. 133). This type and the larviparous type of reproduction have never been met with in the species in Scandinavia (Stephenson 1935, p. 338). The larva is ovate to vase-shaped, 95 to 120 μ long, with a tuft of long cilia at the aboral end (Nyholm 1943, pl. p. 180), and will normally swim about with the aboral end forward already 15 hours after the eggs have been fertilised. The Planula-shape is attained in 1—2 days. Settling 5—7 days after metamorphosis (Nyholm, l. c., pp. 190—191). The Planula larva feeds on phytoplankton. The tentacles develop after the larva has settled (Nyholm l. c.).

Sagartia elegans (Dalyell). Fragmentation by tearing (Stephenson 1929, p. 136). Oviparous (Nafilyan 1912, p. 21). Viviparity unknown (Stephenson 1935, p. 323).

Sagartieton laceratus (Dalyell). Fragmentation by constriction (Stephenson 1929, p. 137); sexually ripe in the autumn near Bohuslän (Nyholm 1943, p. 214). Viviparity seems to be unknown (Dalyell 1848). The egg-size and the larvae do not seem to be known.

Sagartieton undatum (O. F. Müller). Asexual reproduction unknown (Stephenson 1935, p. 361). Sexually ripe near Bohuslän in June-July (Nyholm 1943, p. 226). The larvae are small, with only small amounts of yolk, and with a sharply marked aboral end, bearing a tuft of long cilia (Stephenson 1928, p. 76; Carlgren 1906, p. 86). Viviparity does not seem to occur in this species (Stephenson 1935, p. 361).

Metridium senile Linné **dianthus.** Asexual reproduction in more than one way, especially by laceration (Stephenson 1935, p. 228). The species is oviparous near Bohuslän, where it has its breeding season in June-July (Nyholm 1943, p. 212), and also near Millport, where the breeding season is the same (Gemmill 1920 b). The latter author states: eggs opaque, 100 μ across, with a very thin egg membrane, dark greenish-grey to brick-red. "The same individuals spawned several times at longer or shorter intervals (2—10 days)". The Blastulae float in the water, and so do the ovate-cylindrical Planulae with the aboral end forward. "Towards the end of gastrulation a tuft of six or seven long, rather stiff cilia grows out of the apex of the aboral pole from a small group of elongated columnar cells, and these cilia form a striking feature throughout the planula stage. When stretched out the cilia are half as long as the larva itself". . . . "Older planulae tend to remain at the bottom . . .". — Thus the larva shows close similarities to those described for *Sagartia* and *Sagartieton.*

Discussion of the Reproduction in *Thenaria.*

Within the Actinian larvae, which develop tentacles in the 8-mesenterium stage after having settled, Carlgren (1906, p. 86) and Stephenson (1928, p. 75) distinguish between two types of larvae, viz.

1. Relatively large, unwieldy larvae, rich in yolk, and with the cilia almost equally distributed all over the ectoderm. They swim about very slowly and in irregular directions; they remain near the bottom and are not truly planktonic; and

2. Smaller larvae with less yolk, ovate-cylindrical in shape, with a sharply marked aboral end bearing a tuft of long cilia. They swim readily about, the aboral end forward, rotating on their longitudinal axis.

According to the above survey the larvae of type 1 seem to be from 600—1200 μ long. They have a fairly long pelagic life (up to 25 days from fertilisation to settling) and take no food from the plankton, that is to say they are lecithotrophic. Among the species from the Sound belonging to this type are *Bolocera tuediae, Tealia felina coriacea,* and —judging from the egg-size, the egg-type, and the systematic position of the species —the larvae of *Stomphia coccinea.* — A larva of this type from the Sound, which according to its size (600 μ long when contracted, 1000 μ long when stretched out) most likely belongs to *Tealia felina coriacea,* is seen in fig. 6. It has eight mesenteries, black pigment round the margin of the mouth, a reddish-brown disc; the stomach contains yellowish-greenish-brown granules, while the ectoderm and mesenteries are colourless. The mouth is found at the broad end, and during swimming the aboral pole is directed forward. — Larvae of this type are rare in our main series, taken off Ven on $^{18}/_{4}$ 1938 (1 spm.), $^{25}/_{9}$ 1938 (2 spms., probably *Tealia felina coriacea,* cf. fig. 6 A-B), and off Helsingør on $^{7}/_{10}$ 1941 (5 spms.). However, they may have been overlooked in our main series on a few occasions.

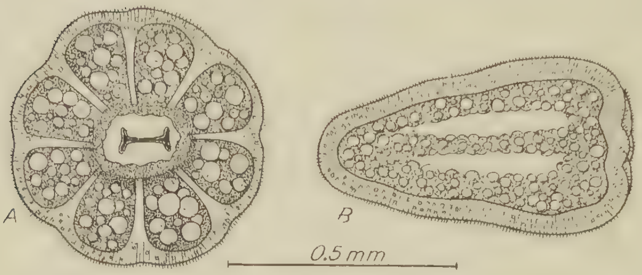


Fig. 6 A-B. Larva presumably belonging to *Tealia felina L.* var. *coriacea* (cf. the text p. 32). From plankton off Ven, depth 18-0 m, caught an drawn from life on $^{25}/_{9}$ 1938. *A.* The contracted larva seen from the mouth. — *B.* Swimming larva (aboral pole forwards) in lateral view.

According to the above survey the larvae of type 2 seem to be 95—300 μ long (see also the remarks below), that is to say they are much smaller than those of type 1. Their pelagic life seems to be rather short, viz. 5—7 days. Their digestive system is formed already during the pelagic stage, and the larvae seem to be able to feed on phytoplankton. — In the Sound larvae of this type seem to occur in *Sagartia troglodytes, Sagartieton undatum,* and *Metridium senile dianthus* (and — in other Danish waters — also in *Sagartia viduata*). *Sagartia elegans* and *Sagartieton laceratus* have probably larvae of a similar type. A larva of this type is seen in fig. 7. It occurred frequently in Limfjord-plankton in the summer of 1940, and belongs most probably to *Metridium senile dianthus,* — which is the absolutely dominant Actinian here. The high cylindric ectoderm-cells are yellowish, the entoderm is brownish. This larva, 300 μ long, is much larger than that of for instance *Sagartia troglodytes,* which is 95—120 μ long, and the ciliary tuft seems to be much shorter than in the latter species. — Carlgren (1906, p. 86—87) states that larvae belonging to this type are so similar from species to species that he has been unable to distinguish them from each other. "When good differences actually occur, they are probably so subtile that they cannot be used in practice" (Carlgren l. c., translated from the German). The differences in size mentioned here may probably help us to distinguish them from each other. — In our main series larvae of this type were taken off Ven on $^{25}/_{9}$ 1938 (1 spm.), and off Helsingør on $^{7}/_{10}$

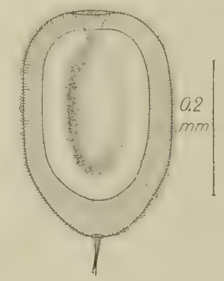


Fig. 7. Larva presumably belonging to *Metridium senile L.* var. *dianthus.* From plankton off Nykøbing Mors (the Limfjord, NW. Jutland) caught and drawn from life on $^{4}/_{7}$ 1940. (Sketch by mag.sc. Erik Smidt).

1941 (5 spms.), $^2/_{12}$ 1941 (2 spms.), and $^4/_6$ 1942 (1 spm.). They may, however, have been overlooked on several occasions.

To sum up, the following types of larval Anthozoans may be found in the Sound:

A. Larvae without tentacles in the pelagic stage:

- I. Large (probably 600—1200 μ long), yolky, lecithotrophic (cf. pp. 436—438) larvae, ovate to pear-shaped and equally ciliated all over the body. No ciliary tuft at the aboral pole. They swim slowly about near the bottom, and may have
  1. A short pelagic life (a few days to a week), viz. in *Alcyonium digitatum* and *Virgularia mirabilis* (this larval type is probably known from plankton taken in the Sound).
  2. A long pelagic life (up to 25 days), viz. in *Bolocera tuediae, Tealia felina coriacea,* and ?*Stomphia coccinea* (this larval type is known from plankton found in the Sound).
- II. Small (95—300 μ long), planktotrophic larvae, ovate-cylindric to vase-shaped, with a tuft of long, rather stiff cilia at the aboral pole. They swim lively about, they feed on phytoplankton, and their pelagic stage is very short, e. g. *Sagartia troglodytes, Sagartieton undatum,* and *Metridium senile dianthus* (this larval type is known from plankton taken in the Sound).

B. Larvae with tentacles in the pelagic stage.

- I. Rather small (probably 250—400 μ long), lecithotrophic larvae, ovate-cylindric, with a long tuft of cilia at the aboral pole and with a few (up to four) equally long tentacles in the oldest pelagic stage. They have a long pelagic life (up to one month). Hitherto only known from the French species *Edwardsia beautempi,* but it is probably the larval type of several Danish *Athenaria* also. (The larval type is unknown in plankton from the Sound.)
- II. Rather large (500—2500 μ long) planktotrophic larvae, equally ciliated all over the body (no ciliary tuft), with 4—13 tentacles. They feed and grow rapidly during the planktonic stage, which is very long. Example: *Cerianthus lloydii* (this larval type is known from plankton found in the Sound).

2. Polychaeta.

The following authors have contributed to our knowledge of the distribution of the Polychaete fauna in the Sound: Ørsted (1844), Tauber (1879), Levinsen (1883—1884, 1893), Lönnberg (1898, 1899), C. G. Joh. Petersen (1911, 1913, 1914, 1915, 1918), Eliason (1916, 1920, the latter paper including a few of Thulin's unpublished finds), Söderström (1920, *Microspio arctica*), Brattström and Thorson (1941, *Miroserpula inflata*), and E. Wesenberg-Lund (1941, *Fabricia dubia*). The paper of Eliason (1920) must be regarded as the main work dealing with the Sound. During the last few years our investigations have added 16 new species hitherto unpublished from this area to the fauna, viz.: *Autolytus prismaticus, Phyllodoce maculata, Mystides sp.* (old larva only), *Tomopteris helgolandica, Nereis virens, Leptonereis glauca, Scolecolepis ciliata, Poecilochaetus serpens* (old larvae only), *Streblospio shrubsolii, Chaetopterus variopedatus, Lanice conchylega* (fresh tubes and larvae only), *Pista cristata, Chone infundibuliformis, Hydroides norvegica, Serpula vermicularis,* and *Spirorbis borealis.* Further, Dr. Eliason, Göteborg, has kindly informed me that *Gattyana amondseni, Harmothoë Ljungmanni, Harmothoë glabra, Sthenelais limicola, Nephthys incisa, Glycera goesi, Spiochaetopterus typicus,* and *Heteromastus filiformis* have been found in the Sound in recent years (hitherto unpublished). Thus, at present 143 species of *Polychaeta* are known from the Sound.

In spite of the rather copious literature the larval Polychaetes are still poorly known. The figures published are often rough sketches, several of them are even incorrect as regards the number of parapodia, the bristles, the ciliation, the number and shape of the dorsal and ventral cirri, the pigmentation, etc. Further, the majority of the larvae described are only referred to family or genus, but not to species. The compilation of Nolte (1936, 1938) on *Polynoid* larvae and *Phyllodocid* larvae in "Nordisches Plankton" has shown how great the confusion is, and it has not helped much to clear up the problems. The larval development in several large groups of Polychaetes is still entirely unknown, e. g. in the families *Sphærodoridae, Paraonidae, Chlorœmidae, Scalibregmidae, Maldanidae,* and *Ampharetidae.* The mode of development of forms of other families, also, *Aphrodite aculeata, Pholoë minuta,* and *Lumbriconereis fragilis,* all of which are common in the Sound, is quite unknown.

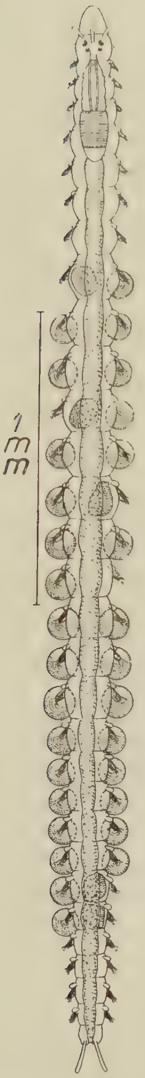
The main works on Polychaete larvae which have been used during the working up of the larvae from the Sound are: Claparède and Metschnikoff (1869), Fewkes (1885), Cunningham and Ramage (1888), Leschke (1903), Gravely (1909 a, b), Herpin (1924 a—b, 1925), and the fine papers of D. P. Wilson (1928 a, 1928 b, 1929, 1932 a, 1932 b, 1933, 1936 a, 1936 b, 1936 c). To these may be added the valuable investigations of: Agassiz (1867), Blegvad (1923), Claparède (1863), Cerruti (1910), Day (1934, 1937), von Draschke (1884, 1885), Eisig (1887, 1899, 1914), Flattely (1923), Fuchs (1911), Enders (1909), Groot (1907), McIntosh

(1869 to 1927), Meyer (1938), Potts (1911, 1913), de Saint Joseph (1887), Söderström (1920), and many others. The paper of Aiyar (1933), which deals with the Polychaete larvae of the Madras coast, is likewise very interesting, being an attempt to trace the Polychaete larvae in the plankton of a certain area and their frequency in the different months of the year. The character of the present investigation made rearing experiments on a large scale — the only method by which safe identifications can be obtained – impossible. Several of our larvae have been referred to their species on the basis of calculation of probabilities only, a method which is especially suitable in the Sound with its northern and southern areas of distribution, and its two distinct water masses. Several of the identifications given here are, therefore, correct, while others are rather uncertain. As the characters on which the identification is based are given in each single case, it may be left to the readers to decide whether or not they agree in the author's conclusions. — Old planktonic larvae of Polychaetes which metamorphose into tube-building forms will often move about constantly when placed under a cover glass and are therefore very difficult to sketch. When the larva is placed into a narrow tube of glass (capillary tube) and this again under the cover glass, the larva will keep much more quiet and thus allow a detailed study of its structure.

The figures have been drawn by the author. During the first two years of our investigation our knowledge of the larvae and the drawing technique employed were so insufficient that the figures from this period must be regarded as rather rough sketches. In the subsequent years up to the present day all the drawings have been very carefully made. Often, a single figure has taken two to four hours; the individual parapodia, tentacles, cirri, ciliary tufts, and pigmentations have been studied in detail and sketched by means of the Abbe drawing apparatus. When possible, the drawings from the first years have been replaced by new, more detailed drawings, which, therefore, constitute by far the majority of the figures. If a figure should be regarded merely as a "rough sketch", this will be stated in the text in each single case.

Exogone gemmifera (Pagenst.). Northern part of the Sound, rather common.

Reproduction: A. Literature. Pagenstecher (1863), de Saint-Joseph (1887), Viguier (1884, good figures), and Potts (1913) have described and figured the brood protection of this species. Malaquin (1893) discusses the earlier literature and adds a couple of new observations. When mature, males as well as females are provided with long bristles. The female has brood protection. The large eggs produced in the body cavity are pressed out through the nephridia, and one egg is attached ventrally to each parapodium, i. e. two eggs per segment. The eggs rich in yolk, in which the egg membrane forms part of the larval cuticle, develop here, not leaving the mother animal until four or five pairs of parapodia as well as eyes, antennae, and a pharynx have developed. When they leave the mother, no cilia are present, and the larvae will at once begin to crawl on the bottom, thus having no pelagic life. — Allen (1915) mentions, from Plymouth, specimens carrying eggs and embryos in June. Ørsted (1845) describes and figures the brood protection of *Exogone naidina* in Danish waters (in the Little Belt off Strib), which species, according to Augener (1939), should probably be regarded as identical with *Exogone gemmifera* Pagenstecher. If, however, Ørsted's figures are correct, this identity seems to be rather dubious. Thus, according to the literature the typical *Exogone gemmifera* has only two ripe eggs per segment (now confirmed by observations in the Sound), while the female figured by Ørsted (pl. II, fig. 4) has no less than 4 or 5 eggs per segment on an average. Such a great difference can hardly be due to an incorrectness in the drawing. Fauvel (1923, p. 305) seems to agree in regarding *E. naidina* and *E. gemmifera* as different



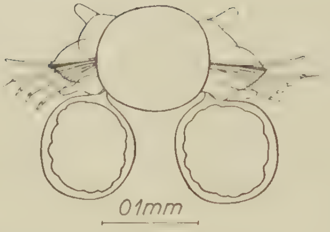


Fig. 8 A-B. *Exogone gemmifera* (Pagenst). Adult female with eggs on segments 8 to 25 (both included). From a bottle-collector exposed off Ven, depth 16 m, from $^{21}/_{7}$ to $^{8}/_{8}$-1940 (drawn from life on $^{8}/_{8}$-40).—Transverse section of the same female showing the adhesion of the eggs below the ventral cirri.

species. He regards *E. gemmifera* Pagenstecher as synonymous with "*E. naidina* McIntosh 1874, p. 108 (non Ørsted)". — Brood protection is known in *E. gemmifera, E. naidina, E. brevipes,* and *E. hebes* (cf. Fauvel 1923, p. 305—309).

B. Own remarks: A bottle collector exposed at a depth of 16 m off Ven from $^{27}/_{5}$ to $^{19}/_{7}$-41 contained a female of *E. gemmifera*, which had ripe purple-coloured eggs in the body cavity. Two eggs were present in each of segments Nos. 8 to 26 (both included), i. e. in 19 segments, while the 5 hindmost segments were free from eggs. The female in question had long swimming setae, and the same was the case with another female (same locality, bottle collector exposed from $^{27}/_{5}$ to $^{17}/_{7}$-41), in which the internal ova commenced in the ninth chaetigerous segment. Such large swimming setae, which seemed to be totally absent in females in the brood protection stage, are probably thrown off as soon as the eggs are extruded and fertilised there (cf. similar conditions in *Sphaerosyllis tetralix*). Another female (from the bottle collector first mentioned) contained young purple-coloured ova with a distinct nucleus in the ninth, the eleventh or twelfth, and the seventeenth chaetigerous segments, and had no swimming setae. The three females examined in July accordingly had internal ova and the brood protection had not commenced. In a bottle collector exposed at Ven at 16 m depth from $^{21}/_{7}$—$^{8}/_{8}$-40 two females inhabiting small tubes of clay were found. One of them carried eggs attached to the ventral cirri on all segments from Nos. 8 to 25 (cf. fig. 8). In some segments one of the eggs was still found in the body cavity, while the other had already been attached to the ventral cirrus. The four hindmost body segments as well as the anal segment were free from eggs. The pink yolky eggs (100 μ in diameter) were in the first stages of development; they were still spherical in shape. A bottle collector exposed in the same locality and at the same depth from $^{24}/_{7}$ to $^{12}/_{8}$-40 contained a male and another female of this species, the latter, like that previously mentioned, with 18 egg-carrying segments and the four hindmost body segments and the anal segment free from eggs. Here, also, the eggs were in the first stages of segmentation. In plankton net hauls (10—0 m depth) from August 1936 a female of this species was captured, the larvae of which were in a somewhat more developed stage though still attached to the mother animal. — Thus the three females with external eggs recorded from Ven were all taken in August, which seems to be the main season for brood protection.

Exogone verugera (Claparède). Northern part of the Sound, rather common.

Reproduction: A. Literature. Fauvel (1923, p. 308) writes about this species: "Reproduction par stolons?". Potts (1911, p. 3), however, mentions *Exogone* among the genera which have "gestation in all forms investigated".

B. Own remarks. A female of *E. verugera* with long swimming setae found near the surface in the Davis Strait, had two eggs per segment attached to the ventrae cirri. (Unpublished, kind information from Mrs. E. Wesenberg-Lund).

Sphaerosyllis tetralix ELIASON. Northern part of the Sound, rather common on soft bottom.

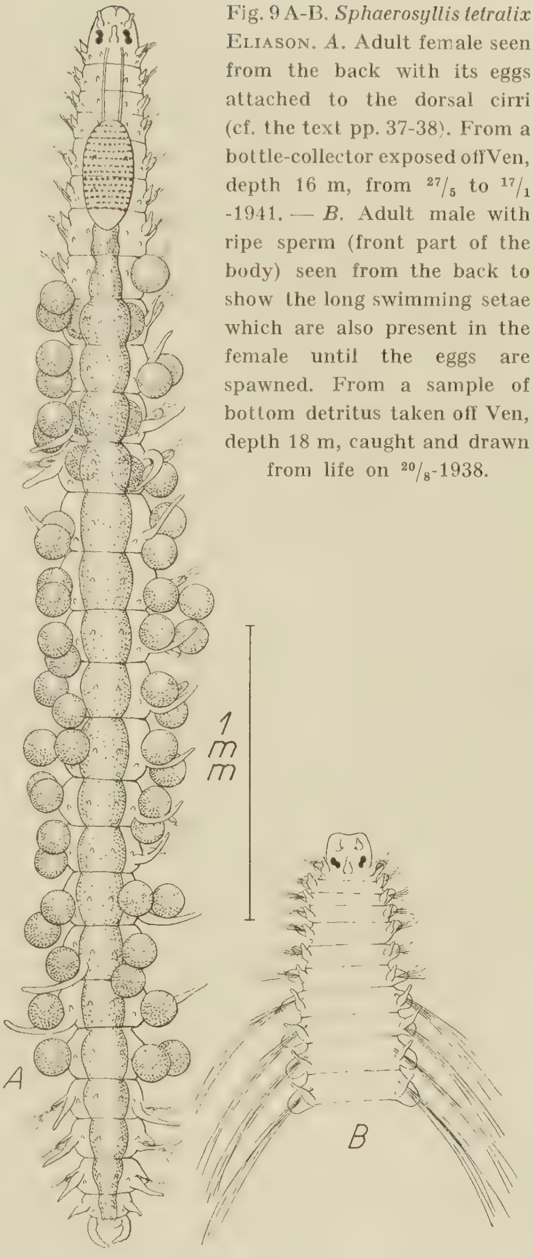


Fig. 9 A-B. *Sphaerosyllis tetralix* ELIASON. *A*. Adult female seen from the back with its eggs attached to the dorsal cirri (cf. the text pp. 37-38). From a bottle-collector exposed off Ven, depth 16 m, from $^{27}/_{5}$ to $^{17}/_{1}$ -1941. — *B*. Adult male with ripe sperm (front part of the body) seen from the back to show the long swimming setae which are also present in the female until the eggs are spawned. From a sample of bottom detritus taken off Ven, depth 18 m, caught and drawn from life on $^{20}/_{8}$-1938.

Reproduction: A. Literature. ELIASON (1920) records a specimen from the Sound, which in each of its segments 10 to 19 (both included) contained two to four large globular bodies which proved to be eggs. The same specimen showed swimming setae ("Pubertätsborsten") on segments 8 to 21. Another of ELIASON's specimens without swimming setae contained egg-like bodies (two to four per segment) much smaller than those mentioned above.—Other species within the genus *Sphaerosyllis* have been well investigated, viz. *S. hystrix* (SAINT-JOSEPH 1887, PIERANTONI 1903, and POTTS 1911); *S. pirifera* (VIGUIER 1884), and *S. erinaceus* (SAINT JOSEPH 1887, ALLEN 1915), all of which have brood protection. In the first two, as in *Exogone*, the large yolky eggs are attached to the ventral cirri, while in the latter species they are attached to the dorsal cirri. Similarly as in the genus *Exogone*, gestation takes place in all forms examined and might therefore also be expected in *S. tetralix*, though it has not hitherto been ascertained.

B. Own remarks. A bottle collector exposed at a depth of 16 m off Ven from $^{27}/_{5}$ to $^{17}/_{7}$-41 contained a large, very characteristic specimen of this species in the first stage of brood protection (fig. 9A). Each of the chaetigerous segments Nos. 8 to 23 (both included) had four eggs on their back. These eggs (0.11 mm. across) were yolky, whitish to pink, and were in the first stages of development. On each side one of the eggs was attached between the setae and the dorsal cirrus, the other egg above the dorsal cirrus. A few of the eggs were still retained in the body cavity. This was the only female found which had reached the stage of external brood protection, and as seen in figure 9A, the female did not show the slightest indication of swimming setae. Two other females, however, found in the same bottle collector, had internal eggs in all the chaetigerous segments from No. 8 to No. 23 (both included, i. e. 16 segments in all), and very long swimming setae from No. 8 to No. 25 (both included, i. e. altogether 18 segments). The eggs in these females proved to be of exactly the same size as those found externally on the female described above. Another specimen with long swimming setae and with 16 segments filled with eggs was taken in a bottle collector, at a depth of 16 m off Ven, exposed from $^{27}/_{5}$ to $^{19}/_{7}$-41, and three females of a very similar appearance and with eggs of the same size were found in bottle collectors exposed at the same depth and in the same locality from $^{5}/_{7}$ to $^{2}/_{9}$-39. All the specimens hitherto mentioned were females. A male found in a sample of bottom detritus derived from a depth of 16 m off Ven on $^{20}/_{7}$-41 was provided with long swimming setae, precisely as it was found in females with internal eggs, and contained large quantities of ripe sperms. Another male (fig. 9 B), likewise with long swimming setae and with ripe sperms, was taken at a depth of 18 m off Ven on $^{20}/_{8}$-38.

Thus at present we know 7 females (including that mentioned by Eliason) of *S. tetralix* with large internal ova and long swimming setae, while the only female found with external ova had no swimming setae at all. A similar variation in the appearance of the females is known for *Sphaerosyllis pirifera*, about which Viguier (1884) writes: "j'ai constaté, chez cette *Sphaerosyllis*, l'existance de males et de femelles mûrs, munis de faisceaux de soies grêles et d'autres qui en etaient depourvus". This seems to show that the ripe females with internal ova swim about in the water seeking a male. Such males, which are likewise provided with swimming setae, will probably meet the females here, and shed their sperms in a cloud around the females. But as the eggs of the swimming females are still retained in the body cavity, where a fertilisation will hardly take place, it must be supposed that the females will press their eggs out through the nephridia at the last moment when a male is present. As will be seen from fig. 9 A, however, some of the eggs are still retained in the body cavity at the time when the majority of them are already exposed on the back of the animal, and it seems difficult to understand how such retained eggs can be fertilised. The facts mentioned above suggest that the female will throw off its swimming setae after fertilisation and sink to the bottom, where it will form a small, sand-incrusted, slime tube, in which it will stay during the period of brood protection. This conjecture is supported by observations on *Eusyllis blomstrandi* (Herpin 1925, p. 148), which can be summarised as follows: swimming at the surface of the water begins in May. The swarming of females begins earlier than that of the males, and the females will not commence spawning until the males have shed their sperms. After spawning, the specimens may throw off their epitoquous setae and continue their life on the bottom. The fact that only females (ripe, but unfertilised) of *S. tetralix* were found in the bottle collectors in July, seems to show that also the females of *Sphaerosyllis tetralix* swarm earlier than the males.

Sphaerosyllis longicauda Webster and Benedict. Northern part of the Sound, rare.

Reproduction: Nothing is known about the reproduction of the species, but our reflections on the preceding species would suggest that this species, too, reproduces by large ova and brood protection.

Syllis armillaris Müller. Northern part of the Sound; not very common.

Reproduction: Nothing is known about the reproduction of this species, but according to Potts (1911) all species of the genus *Syllis* may reproduce by stolonisation.

Autolytus prolifer Müller. Rather rare in the Sound.

Reproduction: A. Literature. The *Sacconereis* produced by stolonisation is provided with a single, very large egg sack on the ventral side, which contains a large number of embryos (Krohn 1852, Potts 1911). Allen (1915) reports, from Plymouth, the occurrence of a specimen with one stolon in May, and a female with many eggs in the body in July. The hatching larvae figured by Okada (1929 b) are provided with two transverse bands of cilia, and pass through a pelagic stage, which according to the figures of McIntosh (1927, fig. 26 to 27) is hardly of long duration. SØREN JENSEN, JOHANSEN, and LEVINSEN (1903) mention the *Saccnereis* of this species from the Skagerak, the Kattegat, and the Belts, taken in the plankton mainly within the period September to December.

B. Own remarks. A beautiful bottom stage with four *Sacconereis* stolons (fig. 10) was taken on *Fucus* at the surface in Helsingør N. harbour (13 $^{0}/_{00}$ salinity) on $^{2}/_{5}$-43, and was, when still alive, handed over to me for drawing and further examination by stud. mag. ERIK RASMUSSEN. The asexual budding specimen had black eyes, brownish-green pigment on the hindmost dorsal part of the head, a line of ochreous pigment flanked the intestine on either side as far as the last segment, and the intestines were filled with small yolky-coloured granules. The stolons were colourless, the hindmost of them only with two pairs of black eyes, with numerous whitish eggs in the distended segments, and with two rather long anal cirri. On $^{11}/_{11}$-41 a *Polybostrichus* (about 4 mm long) was taken in our main series between Hellebæk and Kulla Gunnarstorp, 30 to 0 m, and another *Polybostrichus* was captured in a main series in the same locality on $^{2}/_{12}$-41 (both determined by Mrs. E. WESENBERG LUND). When alive the latter specimen was almost of a verdigris colour, with four black eyes, and swam lively about in the Petri dish. Finally, three free-swimming *Sacconereis* specimens were taken in our main series off Ven on $^{19}/_{10}$-36. All of them were provided with a large ventral sack containing large numbers of larvae. The Sacconereids swam briskly about when placed in aquaria. The larvae in the brood sacks had already eyes and cilia, they moved briskly about, and were nearly ready to hatch. During the whole three-year period of plankton collection off Ven this is the only occasion on which *Sacconereis* specimens were found. The finding has probably some connection with the fact that a violent NW.-gale, which set in three days before the samples were taken, forced large water masses from the Kattegat into the Sound. A *Sacconereis* with its egg-sac was, however, observed in plankton from 40-0 m off Kristineberg (Bohuslän, Swedish W. coast) during a visit on $^{20}/_{8}$-1945 and is sketched here (fig. 11). Free-swimming larvae have never been observed.

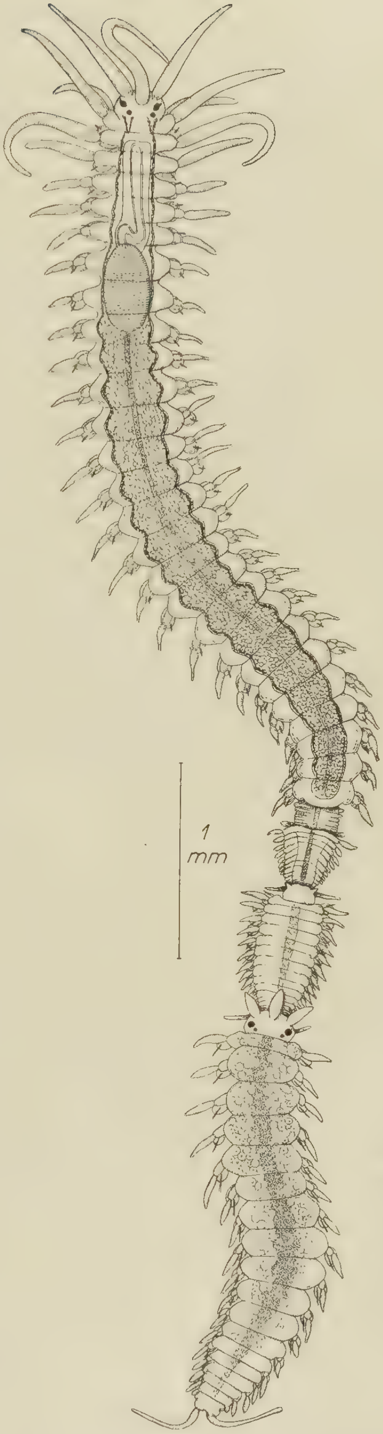


Fig. 10. *Autolytus prolifer* MÜLLER. Bottom stage with four *Sacconereis* stolons. Taken near Helsingør (North harbour) on *Fucus* at the surface, on $^{2}/_{5}$-1943 (Drawn from life on $^{3}/_{5}$-1943).

Autolytus prismaticus (O. FABRICIUS). *Sacconereis* found in a plankton haul between Hellebæk and Kulla Gunnarstorp on $^{11}/_{11}$-41. New to the Danish fauna (E. WESENBERG-LUND det.).

Reproduction: A. Literature. ALLEN (1915) found *Polybostrichus* and *Sacconereis* forms of this species in tow nets off Plymouth in February. The young of one *Sacconereis* kept in the laboratory hatched two weeks later. On $^{18}/_{2}$-1914 OKADA (1929 b), in a tow net in the same locality, found a *Sacconereis* with two egg sacks, from which the larvae hatched on $^2/_3$. He figures larvae one day, three days, and four days old. The ciliary rings have very short cilia — a fact which seems to show that the pelagic stage, if any, is extremely short.

B. Own remarks. The only specimen collected, viz. a *Sacconereis* found in plankton between Hellebæk and Kulla Gunnarstorp on $^{11}/_{11}$-41, was taken in a water column from 30 to 0 metres. It was about 5 mm long, had no egg sack, nor were eggs seen inside the body wall. This seems to show that the stolons begin their free-swimming life a good time before they reach the stage of maturity, and compared with that from the Sound the finds from Plymouth suggest a breeding season in the winter months.

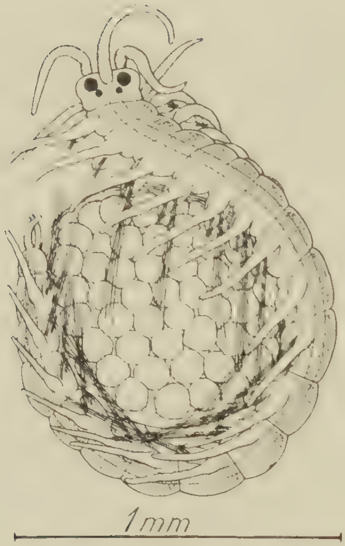


Fig. 11. *Autolytus prolifer* Müller. Sacconereis with its egg-sac. From plankton off Kristineberg (Bohuslän, Swedish W.coast), depth 40-0 m, caught and drawn from life on $^{20}/_8$-1945.

Ephesia gracilis Rathke. Found throughout the Sound, common in the northern part.

Reproduction: A. Literature. Entirely unknown, not only in the genus *Ephesia*, but in all *Sphaerodoridae*.

B. Own remarks. Ripe, or nearly ripe, females were found in large numbers on $^{13}/_9$-41 on the muddy shell banks off Hellebæk, depth 35 m. One of the ripe females spawned when stirred in a glass dish, and the eggs spawned were of precisely the same size as those of other females which were entirely distended by eggs. The eggs shed (fig. 12) were greyish white, discoidal; the vitelline membrane was very thick, and seemed to consist of several lamellae. The content of yolk was rather large. The largest egg diameter was 215 μ (the vitelline membrane 10 μ thick), i. e. a rather large egg, which, after all, will develop in a non-pelagic way. Five females secured in the same locality on $^2/_{12}$-41, and examined alive, had only a few, very small, undeveloped eggs in the body cavity. The spawning season seems, thus, to be limited to the period September-November, which is also the spawning time for most other species living at this depth.

Fig. 12. *Ephesia gracilis* Rathke. Ripe egg seen in its largest diameter, spawned in a glass jar by a female which was stirred. The animal together with several other ripe animals was taken off Hellebæk, depth 35 m, on $^{12}/_9$-1941, and the egg was drawn from life on the same day.

Sphaerodorum claparèdei Greeff. Middle part of the Sound, rather common.

Reproduction: Unknown.

Sphaerodorum philippi Fauvel. Very common in the northern and middle parts of the Sound.

Reproduction: Unknown.

Microphthalmus (Podarke) aberrans Webster and Benedict. Known from two localities within the Sound.

Reproduction: A. Literature. Nothing is known concerning this species. — Viguier (1907), however, has described a *Trochophora* larva presumably belonging to the *Hesionidae* (genus not known). His identification is based on the fact that the larva in question showed a fusion of the four postoral segments — a feature typical of the *Hesionidae*. The larvae captured with plankton nets at a depth of 60 m off France were rather large (3.5 mm long, largest breadth 2 mm), transparent, with orange and white pigment, and showed not the slightest adaption to a pelagic life, swimming only by the aid of the ciliary rings.– Treadwell (1897) mentions that a whole population of ripe specimens of *Podarke obscura* kept in a dish was apt to explode if one started spawning. Such "epidemic spawning" seems mainly to occur in species which shed their eggs freely in the water. This is in good agreement with what is known about another Hesionid, *Ophiodromus flexuosus* (which see).

B. Own remarks. Larval types similar to those described above have not been observed in plankton from the Sound.

Ophiodromus flexuosus Delle Chiaje. Northern part of the Sound, rather common.

Reproduction: A. Literature. McIntosh (1908, monogr., pag. 119) gives the following comments on the reproduction of this species: "A large number of orange-coloured ova were emitted from a ruptured female in August, and those procured by Canon Norman off Bergen, Norway, in July showed the same feature. The ova are comparatively large". Claparède (1870) states that "the ova of the Mediterranean examples were of a greenish-brown colour, and 0.11 mm in diameter".

B. Own remarks. Nothing is known about the reproduction of this species in the Sound.

Castalia punctata Müller. Northern part of the Sound, very common locally.

Reproduction: A. Literature. McIntosh (1908, monogr., p. 124) records large pink ova in specimens examined in September.

B. Own remarks. About 15 large specimens of *C. punctata* taken off Hellebæk, 35 m, on $^{12}{}_{9}$-41 were nearly all females with not fully ripe reddish-purplish eggs in the distended parapodia.

General Remarks on Polynoid Larvae.

The compilation of Nolte in "Nordisches Plankton" (1936) on Polynoid larvae testifies to the great confusion that prevails in the literature concerning this group, and Nolte himself has not contributed very much to clear up these difficult problems. Several Polynoid larvae are described in the literature, most of them, however, without having been identified. Thus on the basis of the numerous descriptions of *Harmothoë* larvae from different localities not a single older larva can be referred with certainty to its adult species, and accordingly each single larva from each single locality is described by Nolte under a provisional name. Numerous figures, all more or less incorrect, and accordingly difficult to recognise merely serve to further obscure the picture.

As our investigations in the Sound were made for ecological purposes, and as we could only work for one or two days on these problems in every two weeks, only a few rearing experiments have been made, so this paper, also, has large lacunae, and many problems as to the Polynoid larvae remain unsolved.

Two of our results seem, however, to be quite certain, viz. the identification and description of the older larvae of *Harmothoë imbricata* — the commonest Polynoid in the Sound — and the ascertainment that *Aphrodite aculeata* has a very short pelagic life or, more probably, a non-pelagic larval development.

Thus the *Harmothoë* larvae are known, but in addition three other types of Polynoid larvae have been found in our samples, two of them even in several specimens. A precise identification of these larvae seems, unfortunately, to be impossible at present. One of the rather common forms may be referred with fairly great probability to *Lepidonotus,* but no definite proof can be given.

Nolte (l. c. p. 80) gives the characteristics of the *Nectochaeta* larvae belonging to the *Lepidonotus* type, and those of the *Harmothoë* type, as follows.

Lepidonotus type: Prostomium kidney-shaped ("like two pears squeezed together"); ends of prostomium converging or parallel; the cirrophores of the lateral tentacles take their rise from the terminal part of the prostomium, i. e. they form direct prolongations of the ends of the prostomium.

Harmothoë type: Prostomium not kidney-shaped, with more or less divergent frontal horns; the cirrophores of the lateral tentacles take their rise from the ventral part of the prostomium.

"Polynoid larva A" (fig. 13) taken off Ven on $^{13}/_{7}$-39; sketched correctly in every detail (the elythra have been lost), seems to agree well with the description of *Lepidonotus* given above. The terminal lateral tentacles as well as the kidney-shaped prostomium are very distinct. The larvae of *Gattyana cirrosa,* however, adult specimens of which are also common in the Sound, are likewise unknown, but as the prostomium of the adults is of the *Harmothoë* type, the larvae of this genus hardly have a kidney-shaped prostomium. It seems justifiable, therefore, to refer the larvae figured to *Lepidonotus squamatus* (the only species of this genus found in the Sound). A description of this larva is given on p. 44.

"Polynoid larva B" (fig. 14, taken off Ven on $^{12}/_{3}$-38 (3 larvae found); must be regarded as a rather rough sketch) has the same kidney-shaped head as the larva here referred to *Lepidonotus.* However, the former larva is larger, which agrees well with the size of its palps and its lateral tentacles as compared with the *Lepidonotus* larva (fig. 13). The latter, however, though smaller than the larva shown in fig. 14, has one pair of distinct tentacular cirri, which seem to be missing in the older larvae of Polynoid B. These tentacular cirri may have been hidden under the ventral side and may accordingly have been overlooked in the rather rough sketch. This larva has also lost its elytra before it was sketched. For a description of this larva, see p. 44.

"Polynoid larva C" (fig. 15). Several specimens, all Nectochaetes, occurred in a main series from Ven, 18 to 0 m, taken on $^{1}/_{7}$-43. They have not been ascertained with certainty in our four years' samples from the Sound, but they may have been overlooked, and, if so, placed among the *Lepidonotus* larvae (not among the *Harmothoë* larvae). The figures were very carefully drawn, and are correct even in the details. The occurrence of several larvae in a single sample seems to show that the larvae belong to a species the adults of which are rather common in the Sound or southeastern Kattegat. As two of the commonest species, viz. *Harmothoë imbricata* and *Lepidonotus squamatus,* must be left out of consideration, it seems most reasonable to refer these larvae to a third species which is likewise very common in the Sound, viz. *Gattyana cirrosa.* This is all the more natural, since the larvae in question seem to bear a much greater resemblance to the *Harmothoë* type than to the *Lepidonotus* type, and the prostomium of the adult *Gattyana* belongs to the *Harmothoë* type. For the description of this larva, see p. 45.

"Polynoid larva D" (fig. 16). Only one larva is at hand from a single main series taken off Ven on $^{23}/_{10}$-37. The sketch is probably rather rough, but owing to the position of the eyes and the two dark brownish swellings on the ventral side behind the prostomium the larva is easily distinguishable from those of other Polynoids found in the Sound. The larva, which is 480 μ long (anal cirri not included), is a *Nectochaeta* with seven chaetigerous segments. Its colour is greyish-brown, and its eyes are black. We have no idea of the identity of this larva, which seems to be rather rare in the Sound.

Aphrodite aculeata LINNÉ. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. The larval development seems to be entirely unknown. LO BIANCO (1899) observed males of this species spawning in aquaria at Naples in March. CERRUTI (1921) observed spawning animals in January and February in the same locality, and McINTOSH (1900, monogr.) states that at St. Andrews the species has abundant ova in May, and adds that "the larvae have not been seen".

B. Own remarks. The development of this common species is quite unknown. According to the literature cited above the species seems to spawn in the winter and spring (January to May). As mentioned above, it is very common in the Sound, and the larvae, when pelagic, might be expected to occur rather commonly in the plankton like the larvae of other common species of Polynoids with pelagic larvae, i. e. *Harmothoë*, and ?*Lepidonotus*. However, during the whole four-year period not a single Polynoid larva was present in the samples either from the winter, the spring, or other seasons, which could be referred to *Aphrodite aculeata*. The few unidentified larvae of Polynoids found in our plankton hauls were all provided with lateral tentacles, which do not occur in the adult *A. aculeata*. The species must accordingly be assumed to have a very short pelagic stage, or, more probably, a non-pelagic larval development. The only species within the *Hermioninae* the larval development of which is known, viz. *Hermione hystrix* (cf. VON DRASCHKE 1885), has, curiously enough, a rather long pelagic life.

Laetmatonice filicornis KINBERG. Found at Hornbæk by ØRSTED 1840. Not found in recent years.

Reproduction: A. Literature. McINTOSH (1900, mgr.) states that "Ova of considerable size are present in examples dredged by Dr. GWYN JEFFREYS off North Unst in June, 1867". This is the only observation which I have been able to find in the literature.

B. Own remarks. As this species has not been found in the Sound since the investigations of ØRSTED 1840, it is now probably totally absent from, or at least extremely rare in, the Sound. Accordingly nothing is known about the reproduction of this species, but the "ova of considerable size" mentioned by McINTOSH suggest that the larval development is non-pelagic like that of *Aphrodite aculeata*.

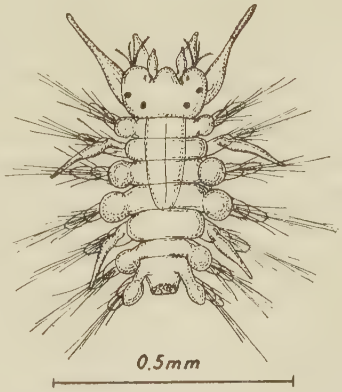


Fig. 13. "Polynoid larva A", presumably belonging to *Lepidonotus squamatus* LINNÉ (see the text pp. 44). *Nectochaeta* from plankton off Ven, 18 to 0 m, on $^{13}/_{7}$-1939 (drawn from life the same day. Some elytra have fallen off).

Lepidonotus squamatus LINNÉ. Northern and middle parts of the Sound, common.

Reproduction: A. Literature. McINTOSH (1900, mgr.) describes and figures the spermatozoa. Off Scotland he has seen specimens with ripe eggs in May to August. He supposes the main spawning to be in June-July. AUGENER (1939) records a ripe male from the Baltic from July. The egg size seems to be unknown. NOLTE (1936)

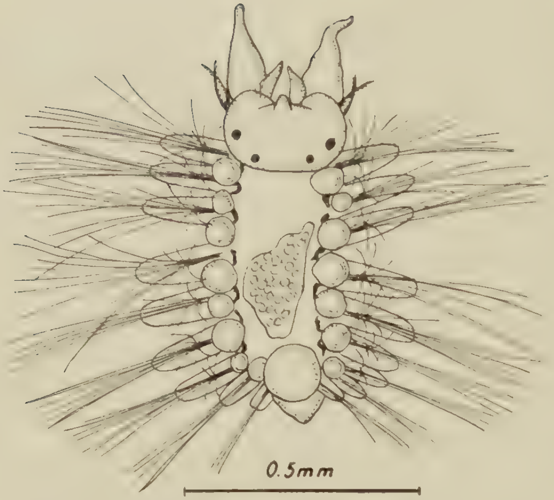


Fig. 14. "Polynoid larva B", probably belonging to *Lepidonotus squamatus* Linné (see the text p. 44). *Nectochaeta* taken in plankton off Ven on $^{12}/_{3}$-1938 (drawn the same day from a dead specimen. Rather rough sketch. Elytra fallen off).

states that the larva referred by Leschke (1903) to *Lepidonotus* is actually the larva of a species of *Harmothoë*. Nolte (l.c. p. 80) further summarises the characteristics which distinguish the larvae of *Harmothoë* from those of *Lepidonotus* (see the present paper, pp. 41—42).

B. Own remarks. The larvae of *Lepidonotus squamatus* have not yet been described. Reasons given in the present paper on p. 42 seem to show that the "larval Polynoid A" fig. 13 taken off Ven in the main series on $^{13}/_{7}$-39 should very likely be referred to this species, though no unmistakable evidence is at hand. The larva (fig. 13) is a *Nectochaeta*, 480 μ long, it has 7 chaetigerous segments, Nos. 2 and 5 of which bear dorsal cirri. Two pairs of black eyes, two small points of black pigment at the base of the terminal, lateral tentacles on a yellowish-brown kidney-shaped prostomium. The body is greyish-brown with dark-brown pigment round the anus. The elytra—4 pairs, to judge from the elytrophores—are cast off.

The "Polynoid larva B", taken in three specimens off Ven in a main series on $^{13}/_{12}$-38 (fig. 14, rough sketch only), may also belong to *Lepidonotus squamatus* (for the reasons for and against see this paper p. 42), and will accordingly be described here. It is a *Nectochaeta*, 705 μ long, with 9 chaetigerous segments. The head is kidney-shaped (*Lepidonotus* type), but the tentacular cirri are absent or have been overlooked. Probably some of the dorsal cirri (drawn in the first stage of dissolution) have also been taken for elytrophores. Two pairs of black eyes. The body is greyish-brown. A spot of black pigment at the base of each parapodium.

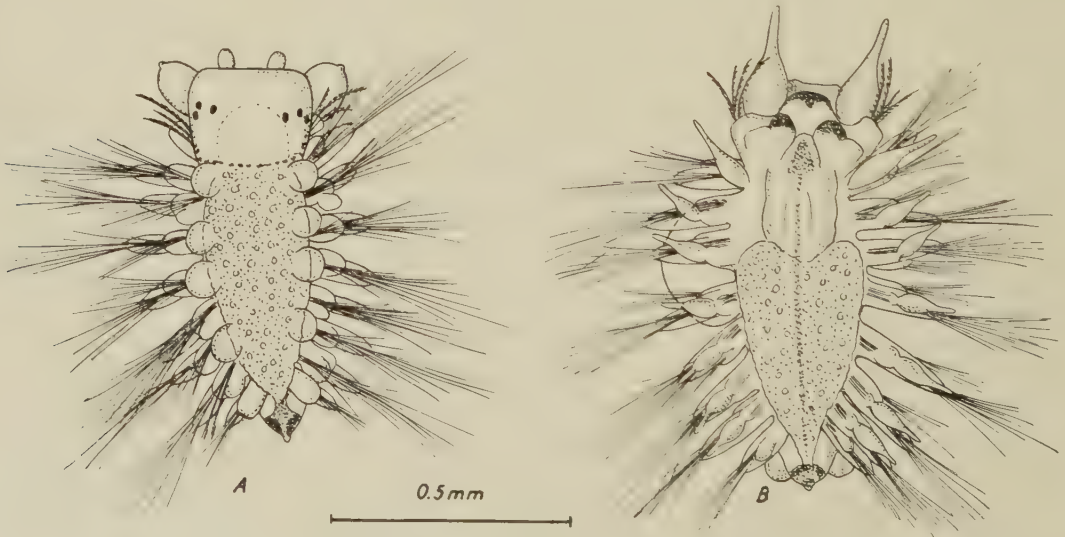


Fig. 15 A-B. "Polynoid larva C", presumably belonging to *Gattyana cirrosa* Pallas (see the text p. 42). From plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{1}/_{7}$-1943. A. *Nectochaeta* seen from the dorsal side (elytra fallen off)- B. Large *Nectochaeta*, seen from the ventral side. The elytra are still present.

Unfortunately no distinction between larvae of "Polynoid A", and "Polynoid B" was made in our main series, all the more so since the typical "Polynoid larva A" was isolated and figured as late as July 1939. The dates of occurrence for each of these larvae cannot, therefore, be seen from our main series. Besides the dates mentioned above for each of the two types, larvae of the common types were met with off Ven on: $^{3}/_{4}$-38; $^{18}/_{4}$-38; $^{6}/_{6}$-38; $^{10}/_{4}$-39, but these records may also comprise specimens of the "Polynoid larva C", which possibly belongs to *Gattyana cirrosa* (see this species).

Gattyana cirrosa PALLAS. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Nothing known. The shape of the prostomium in the adults is of the *Harmothoë* type, and accordingly the larva must be supposed to bear a closer resemblance to those of *Harmothoë* than to those of *Lepidonotus*. See further this paper p. 42.

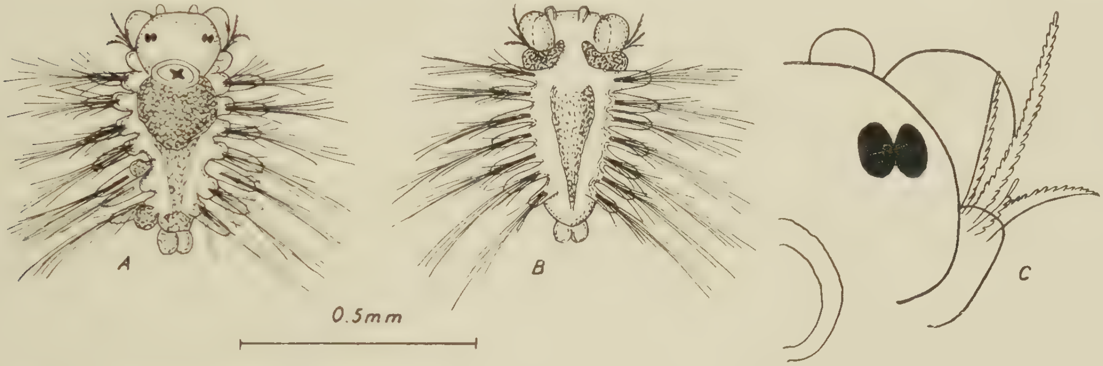


Fig. 16 A-C. "Polynoid larva D", closer identity unknown (see the text pp. 42–43), *Nectochaeta* from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{25}/_{10}$-1937 (Rather rough sketches). — *A*. From the dorsal side. — *B*. From the ventral side. — *C*. Right side of the head more highly magnified.

B. Own remarks. The "Polynoid larva C" (fig. 15) may belong to this species. This is, however, only a conjecture. The reasons for and against are given in this paper p. 42. The larvae in question (fig. 15) are large Nectochaetes, 790 to 800 μ long, with 8 chaetigerous segments. Two lateral tentacles (the median tentacle not yet formed), and two large palps. Three pairs of black eyes. Elytrophores on first, third, fourth, and sixth chaetigerous segment. Ventral cirri on all parapodia. The body is of a greyish colour with a narrow band of brownish-black pigment on the dorsal side behind the prostomium. The anal segment has a light-brown to dark-brown pigmentation, the lips around the big mouth are provided with bluish-black pigment on their terminal parts, and a narrow stripe of bluish-brown pigment is found along the middle line of the ventral side. The intestine was filled with small greyish granules. The elytra had normally been thrown off before the larvae were sketched, but in one specimen (fig. 15 B) a single elytron was left. As stated above, this larva was taken in a plankton haul off Ven, 18—0 m, on $^{1}/_{7}$-43. Numerous specimens were taken, all in the *Nectochaeta* stage. The larva has, no doubt, been overlooked in our main series from earlier years, and has most probably been included under the larvae referred to the "Polynoid larvae A and B". Hence, apart from the specimens on the basis of which our sketches were made, nothing can be stated about the occurrence of this larva during the year.

Gattyana amondseni (MGRN.). Northern and middle parts of the Sound (kind information from Dr. ELIASON, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

Harmothoë imbricata LINNÉ. Extremely common in the northern and middle parts of the Sound.

Reproduction: A. Literature. M. SARS (1845) observed spawning near Norway in February to March. The eggs, 50 μ in diameter and surrounded by a gelatinous substance, develop beneath the elytra of the mother animal, and hatch in the *Trochophora* stage, which is the latest stage observed by SARS. Eggs as well as Trochophores are of a purplish-black colour. SÆMUNDSSON (1918, p. 183) records specimens from Iceland, found in April-May, with numerous pink eggs placed between the elytra and the back of the mother animal. IZUKA (1912) near Japan found females which protect their eggs in a similar way. McINTOSH (1900, monogr.) has described and figured the spermatozoa and the eggs (the latter 0.56 to 0.78 mm in diameter), the *Trochophora*, and *Metatrochophora* reared at St. Andrews in March. LESCHKE (1903, p. 129, Taf. 7 fig. 2) mentions and figures, under the name of *Lepidonotus squamatus*, a larva from the Bay of Kiel which according to NOLTE (1936, p. 135) is a typical *Harmothoë* larva, and hence presumably the larva of *H. imbricata*, which is by far the commonest species of *Harmothoë* in that locality. Further, NOLTE (l. c.) in his survey mentions several other larvae which are described and figured in the early literature and which show the characteristics of the genus *Harmothoë* but are not referred to their species. ERIK SMIDT (1944) gives rather rough figures of a *Trochophora*, and a *Nectochaeta* larva from the harbour of Copenhagen, which probably belong to *Harmothoë imbricata*.

B. Own remarks. The old larval stages of *H. imbricata* have never been reared, and those found in the plankton and referred by various authors to this species must be regarded as doubtful. The larva sketched by SMIDT, however, according to the locality hardly belongs to any other species than *H. imbricata*. The type of larva belonging to the genus *Harmothoë* is well known, and larvae of this type are frequently met with in the Sound plankton, here dominating among the Polynoid larvae. All the *Harmothoë* larvae found from young Metatrochophores (fig. 17 A) to old *Nectochaeta* stages with four or five pairs of elytra (fig. 17 C-D) seem to belong to one species only. According to their large number in the plankton these larvae should most probably be referred to *H. imbricata*, which is one of the commonest Polychaetes in the Sound (ELIASON 1920), while the other species of *Harmothoë* are only of rare occurrence there. The *Metatrochophora* I (fig. 17 A) has the broad shape characteristic of Polynoid larvae, and the whole larva has a purplish tint, which seems to be characteristic of eggs as well as of larvae in all stages of this species. The first "buds" indicating the anterior six body segments can already be seen. This stage is nearly identical with the oldest stage described and figured by McINTOSH (1900, monogr., pl. 26 A, fig. 8). The three pairs of black eyes are already found in their characteristic position known from the older Metatrochophores and the Nectochaetes. The umbrella has spots of black pigment. The stomach contains small granular bodies, and is reddish-brown to purplish. The cilia of the ciliary ring are short. The transitional stage between the *Metatrochophora* II, and the *Nectochaeta* (fig. 17 B) is 480 μ long (exclusive of the anal cirri), has seven chaetigerous segments, four elytra on either side, and two broad anal cirri. Along the hindmost margin of the prostomium a brim of black pigment is found on the dorsal side. The ciliary ring still persists, at any rate partially. The intestine has greyish-green contents. The older Nectochaetes (fig. 17 C-D), still with four pairs of elytra and seven chaetigerous segments, are 570—650 μ long. The anal cirri are somewhat more slender, the lateral and median tentacles have commenced to develop, and the large pharynx is distinctly seen. The three pairs of black eyes and the purplish-black brim of pigment along the hind margin of the prostomium are still present. Intestine greyish-purplish.

The larvae in question are present in our samples taken off Ven on: $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{18}/_{6}$-38; $^{1}/_{7}$-38; $^{17}/_{7}$-38; $^{1}/_{8}$-38; $^{11}/_{8}$-38; $^{26}/_{8}$-38; $^{29}/_{1}$-39; $^{4}/_{3}$-39; $^{25}/_{3}$-39; $^{3}/_{7}$-39; $^{12}/_{7}$-39; $^{15}/_{7}$-39; $^{5}/_{8}$-39, and $^{2}/_{9}$-39, and off Helsingør on: $^{17}/_{9}$-41 (5 larvae); $^{7}/_{10}$-41 (1 larva, and 1 metamorphosed bottom stage); $^{25}/_{10}$-41 (1 larva); $^{3}/_{1}$-42 (7 older larvae); $^{31}/_{1}$-42 (2 larvae); $^{10}/_{4}$-42 (12 larvae in all stages); $^{27}/_{4}$-42 (45 larvae in all stages); $^{15}/_{5}$-42 (35 mostly young larvae); $^{4}/_{6}$-42 (2 larvae); $^{20}/_{6}$-42 (26 larvae); $^{6}/_{7}$-42 (6 larvae), $^{18}/_{7}$-42 (41 larvae in all stages); $^{25}/_{7}$-42 (4 larvae); $^{17}/_{8}$-42 (about 40, mostly young larvae), $^{5}/_{9}$-42 (2 larvae, and 2 metamorphosed bottom stages), and $^{3}/_{4}$-45 (several old larvae associated with the surface layer). Thus the larvae have their maximum occurrence in spring, summer, and autumn, while they are rather rare in the winter, but they may occur in any month throughout the year. Young, just metamorphosed bottom stages of *H. imbricata* (cf. fig. 18) are frequently met with in July and August in the surface layer of the level sea-bottom. Such young bottom stages may also metamorphose in midwater, as mentioned above (cf. further pp. 466—467). The young bottom stage (fig. 18A), taken off Ven on $^{11}/_{8}$-38 and hardly 1.5 mm long, is interesting because the median tentacle in still almost undeveloped. The lateral tentacles which, as will be seen from the older Nectochaetes (fig. 17C-D),

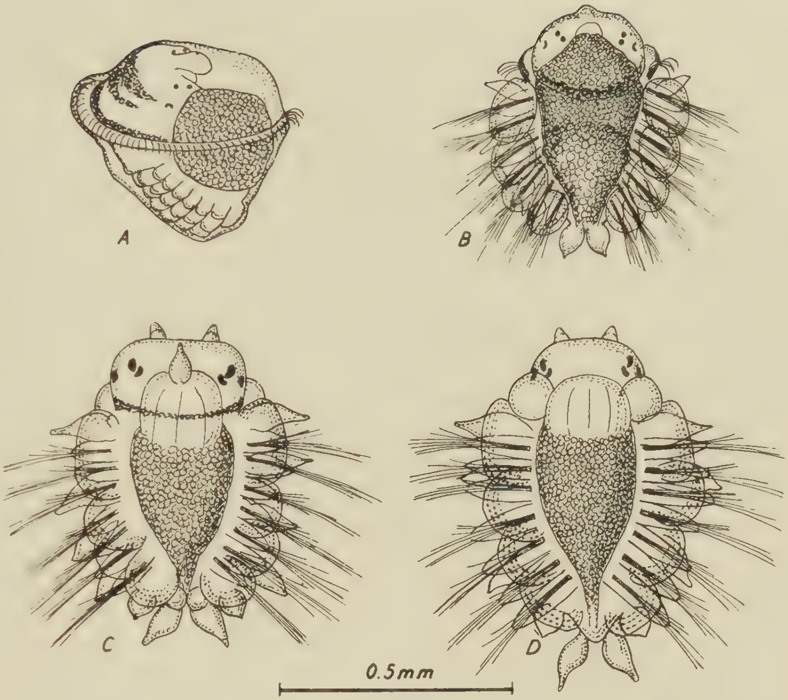


Fig. 17 A-D. *Harmothoë imbricata* Linné. Larvae from plankton off Ven. — *A. Metatrochophora* I ($^{21}/_{1}$-1939). — *B.* Transitional stage from *Metatrochophora* II to *Nectochaeta* ($^{11}/_{8}$-1938). — *C. Nectochaeta* from the dorsal side, and *D.* From the ventral side ($^{19}/_{6}$-1938). All drawn from life on the dates given above.

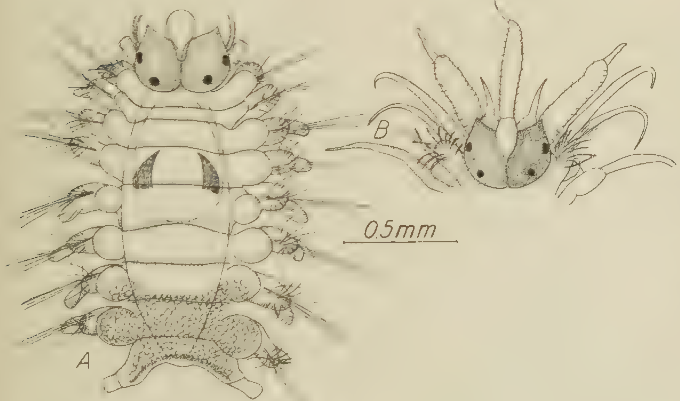


Fig. 18 A-B. *Harmothoë imbricata* Linné. Yong bottom stage taken with a detritus sampler off Ven, depth 18 m, clay bottom. — *A.* Youngest stage found (elytra fallen off). The median tentacle is seen as a bud. Also the pharynx with the jaws is distinct (drawn from life on $^{11}/_{8}$-1938). — *B.* Head of a two and half mm long bottom stage with distinct tentacles and tentacular cirri (elytra not drawn; drawn from life on $^{8}/_{8}$-1938).

have also commenced to develop, are probably hidden on the ventral side of the prostomium. The first traces of jaws are visible. Only two pairs of eyes. A somewhat older stage hardly $2^1/_2$ mm in length (fig. 18 B) had already developed median and lateral tentacles, palps and tentacular cirri. As all stages of developing larvae of this species are frequently found in the Sound plankton, there can be no doubt that at least some of them originate from the Sound itself or its nearest neighbourhood. As mentioned above, *Harmothoë imbricata* is one of the commonest Polychaetes in the Sound, which is in good agreement with the common occurrence of the larvae in the plankton. As, however, *Lepidonotus squamatus* and *Gattyana cirrosa* are also very common in the Sound, though not so common as *H. imbricata*, there seems to be a disproportion between the extremely large number of *Harmothoë* larvae and the relative small number of larvae which should be referred to the other Polynoids. It is not impossible, however, that *Lepidonotus* and *Gattyana* have a somewhat shorter planktonic life than *Harmothoë*, and accordingly a relatively smaller dominance in the plankton. — Dr. H. BLEGVAD has kindly informed me that females of *H. imbricata* with ripe eggs were seen near Nyborg (Great Belt) on $^9/_4$-24 and $^{21}/_3$-25. On $^{18}/_8$-22 a spawning specimen was observed at the surface there. A female with ripe eggs was seen in the Limfjord on $^{15}/_5$-24.

Harmothoë (Actinoë) sarsi KINBERG. Found in the southern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. LEVANDER (1915) records a larva of this genus from plankton taken in the Finnish Gulf, where *H. sarsi* is the only Polynoid known; this shows that the larval stage is pelagic. Dr. H. BLEGVAD has kindly informed me that Polynoid larvae taken by him in plankton in the southern part of the Little Belt on $^4/_{10}$-30 should probably be referred to *H. sarsi*.

B. Own remarks. Nothing is known of this species from the Sound.

Harmothoë (Evarne) impar JOHNSTON. Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. McINTOSH (1900, monogr.) writes that "specimens procured in Norway in summer bear large ova", and that "small examples (about 6 mm) from Loch Portan, Lochmaddy, had advanced ova in August". The same author (1927, p. 76) mentions "pinkish white ova in caelom $^1/_{160}$ of an inch in size, 22nd February", adding that "specimens with ripe ova under the scales were obtained on 17th February. The masses of ova fell off when the animal was interfered with, though they are more or less held together by a transparent secretion". In this connection McINTOSH says that "Young *Polynoidae* are very abundant from June to November in the plankton". Protection of the ripe eggs under the scales seems to be a common phenomenon in the genus *Harmothoë*; it is likewise known from *Harmothoë rarispina* and *H. semisculpta* near Iceland (SÆMUNDSSON 1918).

B. Own remarks. The observations made by McINTOSH (l. c.) seem to indicate that the mode of reproduction of *H. impar* is very much like that of *H. imbricata*. However, nothing is known about the reproduction of *H. impar* from the Sound.

Harmothoë ljungmanni MGRN. Found in the northern part of the Sound. (Kind information from Dr. ELIASON, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

Harmothoë glabra (Mgrn.). Found in the northern part of the Sound. (Kind information from Dr. Eliason, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

Enipo (Polynoë) kinbergi Malmgren. Northern part of the Sound, rather rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Pholoë minuta Fabricius. Very common on soft bottom in the northern and middle parts of the Sound.

Reproduction: A. Literature. McIntosh (1900) describes (without figures) what he supposes to be the Trochophores and Metatrochophores of *Pholoë minuta* from Lochmaddy (taken in September), and figures a young *Pholoë* which has "thirteen bristled feet on each side", taken in a bottom tow-net on February 4th. The description of the *Trochophora* is very insufficient, and no facts are given which prove the connection between this larvae and the adult *Pholoë*. Nolte (1936, p. 89) shows that the *Metatrochophora* described by McIntosh cannot belong to *Pholoë*, but should be referred to another "Polynoid". The post-larval young *Pholoë* with 13 bristled feet, mentioned and figured by McIntosh, seems, however, to be a real *Pholoë*, and to this can be added the following observations of McIntosh (l. c., pp. 441—42): "at St. Andrews ripe males — (of *Pholoë*) — are common at the end of June, so that the breeding-season would seem to be in July and perhaps also in August. On the west coast at Lochmaddy specimens in similar conditions were found in August. No ripe females have been captured at St. Andrews, but examples from Greenland present well-developed ova in July". McIntosh (l. c. pl. 26) also figures the spermatozoa.

B. Own remarks. As mentioned above this species is very common on soft bottom in the Sound, where a large number may be found within a very limited area. The larvae — when planktonic — must be very frequent in the plankton. Furthermore, it may be supposed that the *Pholoë* larva, when planktonic, will bear a fairly great resemblance to those of the *Polynoidae*, the *Sigalionidae* being closely related to these. During the four years' plankton investigations in the Sound, however, no larvae were collected which could be referred to this species. No unidentified Polyonid-like larvae were present in

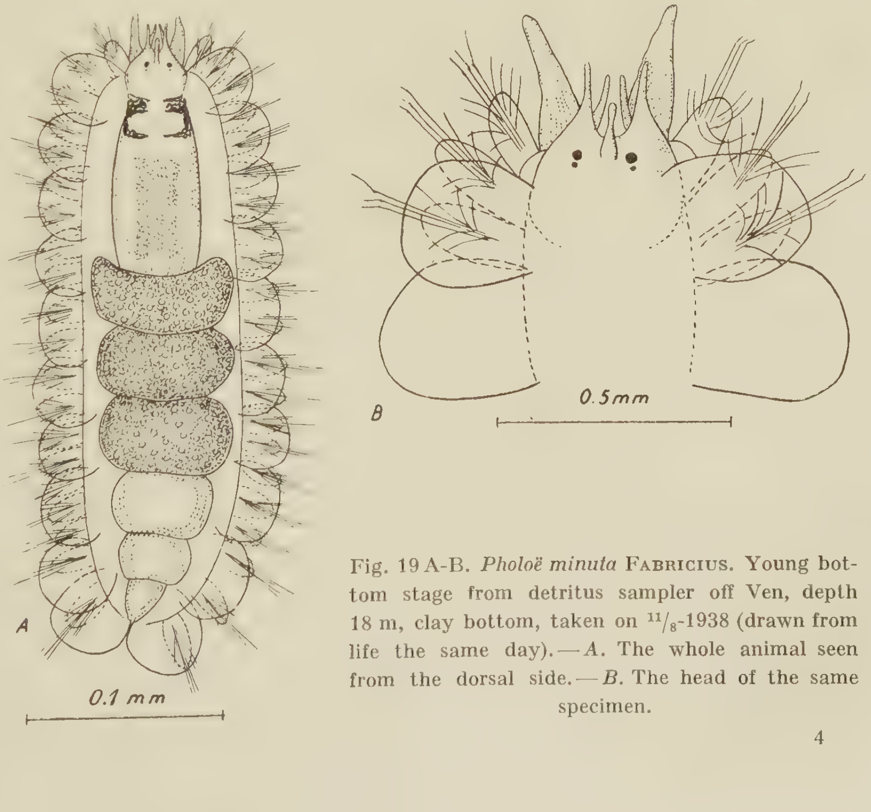


Fig. 19 A-B. *Pholoë minuta* Fabricius. Young bottom stage from detritus sampler off Ven, depth 18 m, clay bottom, taken on $^{11}/_{8}$-1938 (drawn from life the same day). — *A*. The whole animal seen from the dorsal side. — *B*. The head of the same specimen.

such large numbers that they may belong to a bottom animal so dominant, nor were any other larval types found which might even with the slightest probability be identified as *Pholoë minuta*. As it is known with certainty that the species has reproduced in the Sound in the years in which our plankton investigations were carried out (small bottom stages of *Pholoë* $1^1/_2$—2 mm long were frequently met with in the upper bottom layer off Ven in July-August 1938 and in July 1940, fig. 19 A-B), the logical conclusion must be that *Pholoë minuta* reproduces without any pelagic larval stage. The very young bottom stage found by McIntosh in February seems to show that the species may reproduce all the year round — a fact which is in good agreement with a non-pelagic development.

Sthenelais limicola (Ehlers). The specimen from the northern part of the Sound referred by Eliason (1920) to *Leanira tetragona* belongs in reality to *Stenelais* (Kind information from Dr. Eliason).

Reproduction: Unknown in the literature. No observations from the Sound.

General Remarks on Phyllodocid Larvae.

Nolte (1938) writes in his compilation of Phyllodocid larvae in "Nordisches Plankton" that the systematic characteristics of the adults used by Fauvel (1923) are nearly quite useless in the determination of the larvae (l. c. p. 172). Thus the shape and number of eyes of the larvae may be quite different from those of the adults, and genera which, in the adult stage, are characteristic by having a median unpaired tentacle (5 tentacles in all), may lack this essential systematic character in the *Metatrochophora* and *Nectochaeta* stages (cf. Nolte 1938, p. 181). The number of tentacular cirri, however, seems to be a good character of the *Nectochaeta* larva as well as of the adult animals. Thus all the *Nectochaeta* stages of the genus *Phyllodoce* hitherto described have four pairs of tentacular cirri, i. e. the same number as is characteristic of the adult *Phyllodoce*.

In the monograph mentioned above Nolte enumerates 22 species of Phyllodocid larvae derived from benthonic parents (the larvae of species with pelagic adults are not considered here). Of these 22 species 14 are referred by Nolte to the genus *Phyllodoce* and three to the genus *Eulalia* (nearly related to *Phyllodoce*), while one larva, mentioned as "Phyllodocides erinensis", should be referred either to the genus *Eulalia* or to the genus *Phyllodoce*. Thus 18 of the 22 Phyllodocid larvae hitherto described are referred to a group in which all Nectochaetes, like the adults, have four pairs of tentacular cirri. Of the four species left in Nolte's list three belong to the genus *Eteone* (two pairs of tentacular cirri) and one species to the genus *Mystides* (three pairs of tentacular cirri).

On studying the literature on Phyllodocid larvae, it will be seen that the *Metatrochophora* II and the *Nectochaeta* of the genus *Phyllodoce* have a very considerable length (1800 μ and 2000—3000 μ resp.), that those of the genus *Eulalia* are much smaller (*Metatrochophora* II 650 μ, *Nectochaeta* 1000 μ), and that the pelagic larvae of the genus *Eteone* are still smaller (Metatrochophores II of "*Eteone pusilla*" 125 μ, according to Willemoës-Suhm (1871)). In accordance with this the Nectochaetes of the genus *Phyllodoce* (six species examined) had 10, 11, 13, 15, 16, and 30 chaetigerous segments respectively, while the *Eteone-Nectochaeta* had only 5 chaetigerous segments (Leschke 1903). The number of segments in the genus *Eulalia* seems to be intermediate, but the exact number is not given.

In accordance with the above reflections the genera *Phyllodoce, Eulalia*, and probably also *Notophyllum* and *Genetyllis* (two further genera with four pairs of tentacular cirri) might be expected to have a well-developed pelagic larval stage, while in the other genera of Phyllodocids the pelagic stage is much shorter or totally lacking. The last group of genera, i. a. *Eteone*, will then, in spite of their tiny eggs, spend a part or the whole of their metamorphosis in the crawling stage on the bottom. Further, their pelagic stage is probably lecithotrophic (cf. pp. 436—438). As an example I may mention the following observation: a bottle collector exposed at a depth of 16 m off Ven from $^{7}/_{7}$-39 to $^{29}/_{8}$-39 contained a young *Nectochaeta*-like bottom stage of a Phyllodocid, which, though only 390 μ long, had already lost all its cilia and crawled on the bottom (fig. 20). In spite of its crawling stage the specimen had only developed one pair of tentacular cirri (the smallest number known in adult Phyllodocids is two pairs!), and had thus still not completed its metamorphosis. The "*Eteone tocantinsensis*" of REIBISH (cf. NOLTE 1938, p. 241, fig. 171—72), which although it is a post larva has one pair of tentacular cirri only, seems likewise to indicate a non-pelagic or a short pelagic development of several of these forms.

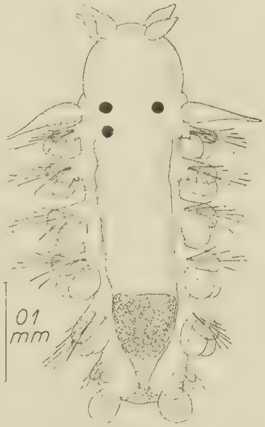


Fig. 20. Young *Nectochaeta*-like bottom stage of Phyllodocid sp. with one pair of tentacular cirri (cf. the text p. 51). From a bottle-collector exposed off Ven, depth 16 m, from $^{7}/_{7}$ to $^{29}/_{8}$-1939 (drawn from life on $^{31}/_{8}$-1939).

Our four years' plankton investigations in the Sound seem to confirm the suppositions mentioned above. During these years several Phyllodocid larvae were taken in our regular samples. The Phyllodocid larvae found belong to three distinct species which were provided with four pairs of tentacular cirri, and to two species with only two pairs of tentacular cirri. Occasional specimens of young stages with one or three pairs of tentacular cirri (i. e. in the crawling stage) were present in the bottom collectors but have never been taken in the plankton. An exception from this rule is formed by the genus *Mystides*, which has actually small, but pelagic larvae. In plankton from Frederikshavn, NW. Kattegat, taken on $^{25}/_{7}$ to $^{31}/_{7}$-39, and off Helsingør on $^{11}/_{11}$-41 I have seen, and sketched, such larvae, viz. Nectochaetes, the oldest 800—900 μ long with 10 chaetigerous segments, four tentacles, and three pairs of tentacular cirri (cf. pp. 62—64, and fig. 28).

The three distinct species with four pairs of tentacular cirri from the Sound differ so much in appearance that they must be supposed to belong to three different genera. One of the larvae can be referred with certainty to *Phyllodoce groenlandica*. Since, moreover, a reliable sketch of the larva of *Phyllodoce maculata* is at hand from Frederikshavn (fig. 22), and several drawings of larvae of *Phyllodoce* are found in the literature, all of which are characteristic by being of a considerable size and having a large "carapace" (shape like a crawfish), it can be stated with certainty that none of the other two forms from the Sound with four pairs of tentacular cirri belong to the genus *Phyllodoce*. As, however, these two larval types likewise differ very much from each other in shape as well as in colour, they must be supposed to belong to two different genera, and I think it justifiable to refer them to the genera *Genetyllis* and *Eulalia* respectively. The reasons for this will be given in the systematic list below.

Notophyllum foliosum M. SARS. Northern part of the Sound, scattered specimens, but not uncommon.

Reproduction: A. Literature. McINTOSH (1908, monogr., p. 49) mentions two females of this species, which "were laden with mature eggs" in August. OKADA (1929 a, pp. 475—479, fig. 1) describes from Plymouth the finding in September 1927 of two females with yellow gelatinous egg-coils placed between the back and the dorsal cirri. The eggs in the coils were in development, and one of the females is figured. Nothing is stated about the egg size, nor is it known whether the primitive brood protection is followed by a pelagic larval stage. The conclusions given above under "General remarks on Phyllodocid larvae" seem, however, to support the supposition that pelagic larvae of this species may occur.

B. Own remarks. The eggs and the larvae of *Phyllodoce* and *Eulalia* are olive-green, while the eggs of *Notophyllum* are yellow. This species may, therefore, be expected to have larvae of a different colour. See, however, the discussion under *Genetyllis lutea* pp. 55–56.

Phyllodoce (Anaitides) groenlandica ØRSTED. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. GRAVIER (1923, p. 174) describes the spawn from France: oval masses, largest diameter 1 cm, attached to algae by a short peduncle. The olive-green eggs are seen through the jelly. Concerning the other *Phyllodoce* larvae and their characteristics, cf. the "General remarks on Phyllodocid larvae" on pp. 50–51. — ELIASON (1920) is of opinion that *Phyllodoce mucosa* and *Ph. groenlandica* belong to one and the same species; in a material examined by the author off Helsingør in the summer of 1941, however, the *mucosa* form was predominant. The free-swimming larvae have not been described.

B. Own remarks. *Phyllodoce groenlandica* is by far the commonest Phyllodocid in the Sound, where it is met with locally in very large numbers, especially at depths exceeding 15 m. The egg masses may frequently be taken in the spring and early summer in localities where the adults are numerous (e. g. off the Kronborg point, Helsingør, 20–25 m), and where *P. groenlandica* is the only Phyllodocid found. Thus, during our investigations in the area Snekkersten-Helsingborg-Viken-Ellekildehage (northern part of the Sound) in June–July 1941 such egg masses were collected on the following dates: ${}^{3-6}/_{6}$; ${}^{12}/_{6}$; ${}^{1}/_{7}$; ${}^{3}/_{7}$, and ${}^{4}/_{7}$, but egg masses with young eggs were also available as early as ${}^{2}/_{4}$-42. In spring and early summer the females are filled with olive-green ova, and a female placed in a glass dish on ${}^{7}/_{6}$-41 spawned the next day; the eggs spawned were of precisely the same size and colour as those spawned under natural conditions. The egg masses (fig. 21 A) are olive-green, gelatinous lumps up to 1 to 1.5 cm in longest diameter. They adhere by their slimy surface or by a short stalk to algae and other substrata. They agree closely with the egg lumps of *Phyllodoce maculata* (M. SARS 1845), from which they can hardly be distinguished. The eggs, 95–105 μ across plus the 8 μ thick egg membrane, are placed irregularly within the slime, and the single egg mass taken off Snekkersten on ${}^{2}/_{4}$-42 contained about 16000 eggs. The olive-green colour of the eggs seems to be a common feature in most Phyllodocid eggs, for a similar colour has been observed in the eggs of several other species, viz. *Phyllodoce maculata* (McINTOSH 1869, p. 2–4, NORDGAARD 1912); *P. lamelligera* (McINTOSH 1908, monogr., p. 80); "*Phyllodoce helderensis*" (cf. NOLTE 1938, p. 208, HORST 1881); *Eulalia viridis* (McINTOSH 1908, monogr., p. 58–59); *Eulalia macroceros* (ibid. p. 62); *Eulalia bipunctata* (ibid. p. 64), and *Eumida sanguinea* (ibid. p. 69).

The larvae (fig. 21 D-E) hatch as large Trochophores, and commence a long pelagic life. They are greyish-olive-green during their whole development, and they attain a very large size. The *Nectochaeta* when fully extended may attain a length of about 3000 μ. In the plankton of the Sound the *Phyllodoce* larvae constitute a rather characteristic element, their size exceeding that of most other Polychaete larvae. The large numbers of larvae in all stages present in our samples have enabled me to make an easy but careful study of the whole development up to

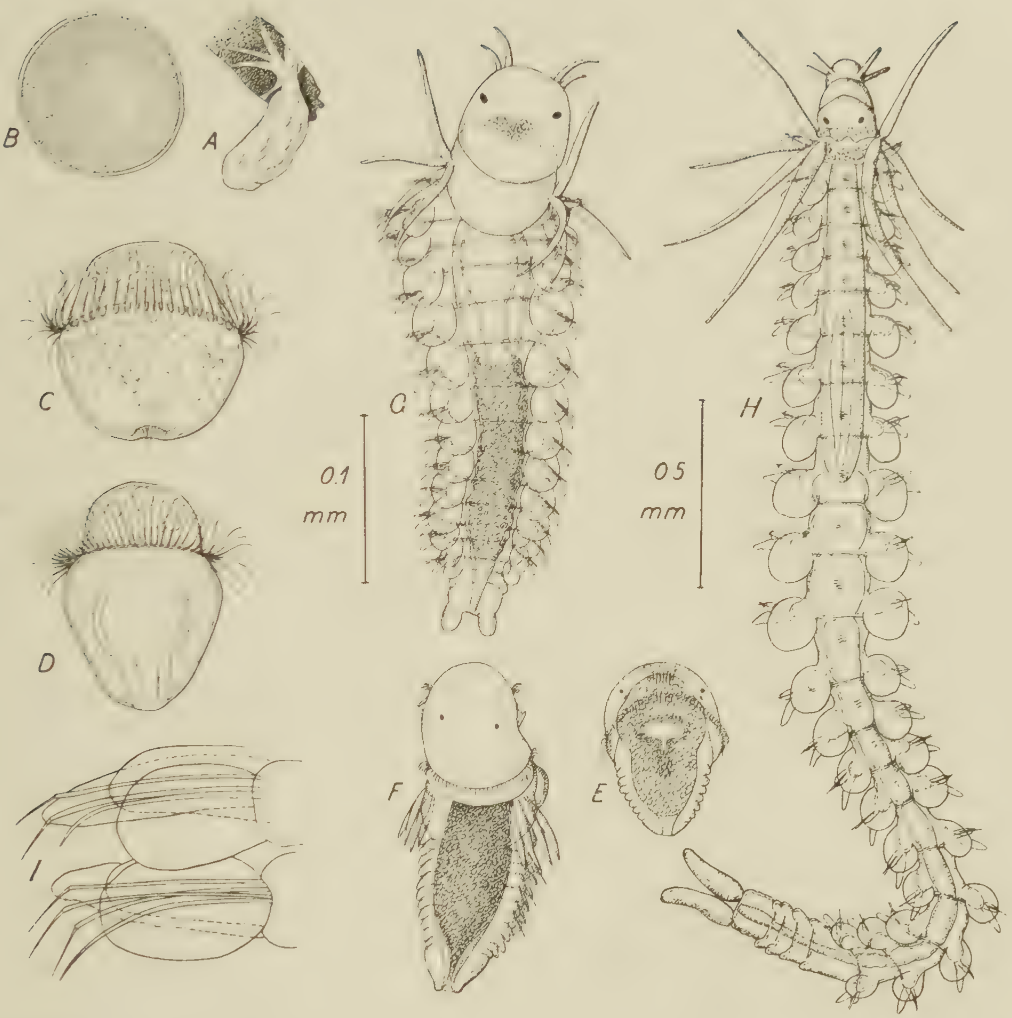


Fig. 21 A-I. *Phyllodoce (Anaitides) groenlandica* Ørsted. Egg-mass and larval development. — *A.* The egg-mass attached to a piece of *Fucus*, off Snekkersten, depth 20 m, on $^{2}/_{4}$-1942 (natural size). — *B.* Uncleaved egg from egg-mass spawned in aquarium on $^{6}/_{6}$-1941 (drawn from life on the same day). — *C. Trochophora*-larva, dissected out from an egg-mass taken in the Sound on $^{5}/_{6}$-1941 and kept in aquarium until $^{8}/_{6}$-41 (drawn from life). — *D.* Old *Trochophora* larva from the same egg-mass (dissected out and drawn on $^{13}/_{6}$-1941). — *E. Metatrochophora* I from plankton off Ven, taken on $^{8}/_{8}$-1942. — *F. Metatrochophora* II from plankton off Ven, caught and drawn on $^{20}/_{7}$-1939. — *G. Nectochaeta* larva from plankton off Ven, caught and drawn from life on $^{12}/_{7}$-1939. — *H.* Young metamorphosed bottom stage taken in an empty tube of *Polydora coeca*, off Ven, depth 10 to 16 m, on $^{12}/_{7}$-1939 (figs. *E* to *H* are drawn from living animals on the dates mentioned). — *I.* Two parapodia from a *Nectochaeta* larva with nine chaetigerous segments. (The 0.1 mm scale refers to figs. *B*, *C* and *D*; the 0.5 mm scale to figs. *E*, *F*, *G* and *H*).

the young metamorphosed bottom stages (fig. 21 D–H). The youngest stage sketched from the plankton, a *Metatrochophora* I (fig. 21 E), taken off Ven, 18–0 m, in a main series on $^{8}/_{8}$-42, is 540 μ long; it has a wide mouth provided with cilia, which continue backwards from the mouth as a broad band on the ventral side. A similar area with finer or coarser cilia is seen at the front end of the "umbrella". Two pairs of dark carmine-coloured eyes. Yellowish-brown pigment round the mouth; greyish to olive-green granules fill the intestine. Seven body segments have commenced to appear. The next larval stage sketched (fig. 21 F) is 940 μ long, and is a *Metatrochophora* II. The four pairs of tentacular cirri and the four tentacles are well developed; 11—12 body segments can be distinguished. Only one pair of carmine-coloured eyes. Two tufts of cilia on the prostomium just above the tentacles; the ciliary ring is still in function. The intestine contains greyish-green granules. Next stage (fig. 21 G), a large *Nectochaeta* 1500 μ long, has 14 chaetigerous segments. All cilia have disappeared. — Finally, a young, just metamorphosed bottom stage 3200 μ long (fig. 21 H) with 24 body segments is sketched. Young of this size may also be found in the plankton (metamorphosis in mid-water, cf. pp. 466—467). This stage has dark-green pigment on the dorsal side of the prostomium and on the next segment and a brownish spot of pigment on each of the body segments.

In our samples taken off Ven larvae of *Phyllodoce groenlandica* were found on the following dates: $^{21}/_{6}$-37; $^{5}/_{9}$-37; $^{18}/_{12}$-37; $^{18}/_{4}$-38 (159 larvae); $^{10}/_{5}$-38; $^{22}/_{5}$-38; $^{6}/_{6}$-38; $^{18}/_{6}$-38; $^{1}/_{7}$-38; $^{17}/_{7}$-38; $^{1}/_{8}$-38; $^{6}/_{8}$-38; $^{13}/_{8}$-38; $^{26}/_{8}$-38; $^{11}/_{9}$-38; $^{25}/_{3}$-39 (55 larvae); $^{10}/_{4}$-39 (365 larvae); $^{30}/_{4}$-39; $^{3}/_{7}$-39; $^{12}/_{7}$-39; $^{15}/_{7}$-39; $^{20}/_{7}$-39; $^{5}/_{8}$-39; $^{18}/_{8}$-39, and $^{16-25}/_{8}$-44, and off Helsingør on: $^{21}/_{2}$-42 (2 young larvae); $^{21}/_{3}$-42 (5 larvae in all stages); $^{15}/_{5}$-42 (1 larva); $^{4}/_{6}$-42 (1 larva); $^{20}/_{6}$-42 (7 *Metatrochophora* II); $^{18}/_{7}$-42 (8 larvae in all stages); $^{25}/_{7}$-42 (5 larvae), and $^{3}/_{4}$-45 (a few larvae). Further, young crawling stages, less than 6 weeks old, were taken in bottle collectors on: $^{2}/_{9}$-39; $^{21}/_{10}$-39; $^{12}/_{8}$-40; $^{18}/_{8}$-40, and $^{17-19}/_{7}$-41. Thus the main season for the occurrence of larvae is from March-April to August-September. After a pause during the whole winter season the larvae will suddenly appear in the plankton, often in large numbers, and this maximum seems to include all stages of development from young Trochophores to Nectochaetes nearly ready to metamorphose, — a fact which makes it probable that the development takes place very quickly. During the late spring and summer, however, only a few larvae (up to 10 or 12) were present in each main series; in late July to early August *Metatrochophora* II and *Nectochaeta* were the dominating stages in the plankton, and in late August only crawling stages already in metamorphosis were present in our samples.

Phyllodoce maculata ØRSTED. A single large specimen was taken between Lappegrunden and Hittarp in the northern part of the Sound, 30—35 m depth, on $^{31}/_{7}$-1941 (E. WESENBERG-LUND det.).

Reproduction: A. Literature. Spawning of this species has been observed at St. Andrews (McINTOSH 1869) and at Bergen and in Oslofjord (NORDGAARD 1912, ?M. SARS 1845) in May and February-March respectively. The egg mass, 2.5 cm in diameter, is bulky, transparent, and gelatinous. The eggs just spawned are grassy-green, about 0.12 mm in diameter. Observations made at Bergen seem to point to a pseudocopulation, i. e. the male and the female may lie close together round a newly-spawned egg mass (no definite proof can be given). The eggs, 3—5 broad, form thread-like bands which are coiled up in the gelatinous substance. Egg masses shed in aquaria at Bergen on $^{28}/_{3}$ had rotating embryos on $^{3}/_{4}$ and free-swimming pelagic larvae on $^{16}/_{4}$. In egg masses shed at St. Andrews (in May, probably at much higher temperatures than in February-March at Bergen) the embryos hatched already two days later, when they were seen to swim slowly along the bottom of the aquarium. When three days old, the eyes were formed, and the larvae swam lively about. When four days old, they swam still quicker. At the end of a fortnight they all showed a tendency to perish. McINTOSH (1869) figures the spermatozoa, the eggs, and the young larvae. AGASSIZ (1867) figures the older larval stages of *P. maculata* from the east coast of North America: Metatrochophores and Nectochaetes with 10 and about 28 chaetigerous segments respectively, with four antennae, four pairs of tentacular cirri and the "carapace" on the dorsal side characteristic of the Metatrochophores of *Phyllodoce*.

B. Own remarks. The larva of this species has never been observed in the Sound. Plankton taken off Frederikshavn, NW. Kattegat, at a depth of 6—8 m on $^{31}/_{7}$-39 contained several Nectochaetes and younger stages of a species of *Phyllodoce*. As the larvae differed from those of *P. groenlandica* and agreed well with the figures given by Agassiz (l. c.), and as *Phyllodoce maculata* is the absolutely dominant species of *Phyllodoce* off Frederikshavn, where it is very common, I have no hesitation in referring the larvae in question to that species.—The larva (fig. 22), 1120 μ long, has 12 chaetigerous segments, four antennae, four pairs of tentacular cirri, a prototroch with short cilia, two large black eyes, olive-green prostomium and peristomium, the hindmost part of the intestine of a verdigris colour and two parallel rows of pigment spots (yellow in direct light and dark olive-green in transmitted light) on the dorsal side of all the segments from the peristomium (included) to the anal segment (excluded). This pigmentation, which was observed in all the larvae examined, makes the larva easily distinguishable from that of *P. groenlandica*. Two small anal cirri.—Younger stages have unfortunately not been sketched.

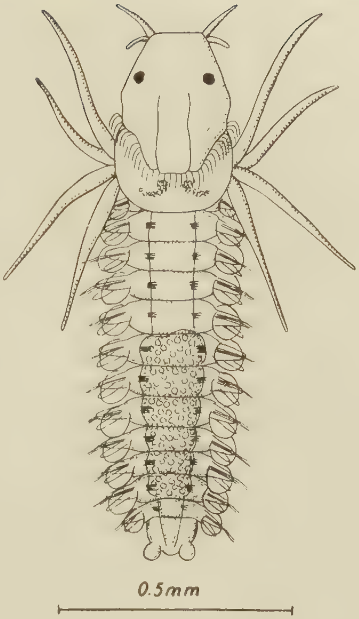


Fig. 22. *Phyllodoce maculata* Ørsted. Old larva from plankton off Frederikshavn, NW. Kattegat, depth 6 to 8 m, caught and drawn from life on $^{31}/_{7}$-1939.

Genetyllis lutea Malmgren. Northern part of the Sound, rare.

Reproduction: A. Literature: Unknown.

B. Own remarks. The larvae shown in fig. 23 A—D were pink with four black eyes, with a rusty-red band of pigment behind the prostomium, and just caudally to this pigment band some reddish-black chromatophores (pink in direct light), which when contracted closely resemble eyes, while in a dilated condition they are branched. Carmine pigment spots are seen on each chaetigerous segment ventral to the parapodia, and a beautiful wine-red colour dominates in the rectum and on the anal segment. Among the adult Phyllodocids in the Sound this colour agrees most closely with that of *Notophyllum* or *Genetyllis*, the *Eulalia* species being brownish or greenish.

At first, therefore, I was most inclined to refer these larvae to *Notophyllum*. In August 1943, however, I had the possibility, in Gullmarfjord plankton to find all transitional stages from the larvae of the Sound (fig. 23 A—D) to old *Nectochaetas* nearly ready to metamorphose (fig. 23 E), and in spite of careful search these old larvae showed not the slightest trace of a median, unpaired tentacle. In such old larvae, if really belonging to *Notophyllum*, the median tentacle would hardly have failed to appear at least as a bud, although such median tentacles seem to appear very late (cf. Gravely 1909; larva of *Eumida sanguinea*). Hence, it seems most reasonable to refer the larvae in question to *Genetyllis*, the adults of which are often red (Eliason 1920, p. 25) like our larvae. But still it cannot be excluded that the larvae may belong to *Notophyllum* (both species are common at Bohuslän).

The stomach and the main part of the intestine are grey. Ciliation: ciliary hook, rudiment of prototroch, and telotroch (cf. fig. 23 A—D). Four pairs of well-developed tentacular cirri. Only the first pair of tentacles is visible in front of the prostomium. The second pair of tentacles had not developed in the young larvae. When irritated, the larva will immediately put out its large pharynx (fig. 23 D), which will soon after be withdrawn and reveal a very large mouth on the ventral side. A similar large mouth is described and figured by AGASSIZ (1867) in his "*Phyllodoce maculata* larva" (cf. NOLTE 1938, p. 190, fig. 112).

The old *Nectochaeta* (fig. 23 E) was 1200 μ long with 13 chaetigerous segments. The prostomium had four distinct tentacles and two reddish-black eyes. Just anterior to the ciliary ring the prostomium has a transverse band of orange pigment. The small "carapace" is pink with small spots of carmine pigment and two similar reddish-dark (pink) chromatophores as in the younger larvae. The four tentacular cirri are long and slender. Two further chromatophores (on the last chaetigerous segment) and an anal ciliary ring are present. The whole body has a pink tinge.

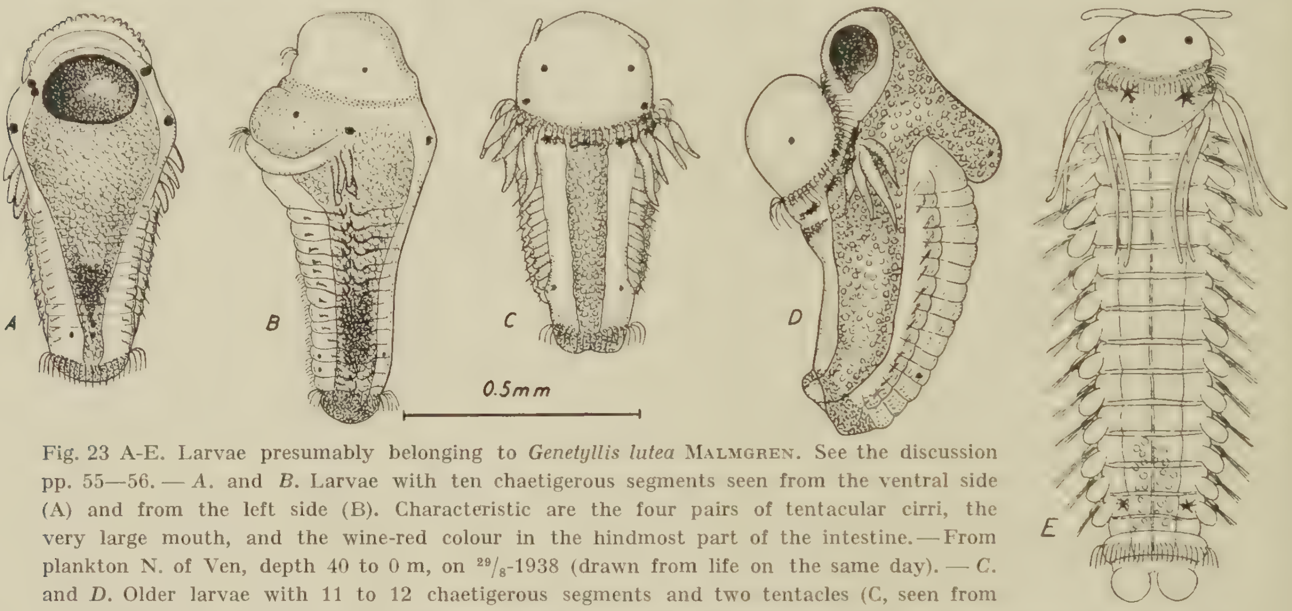


Fig. 23 A-E. Larvae presumably belonging to *Genetyllis lutea* MALMGREN. See the discussion pp. 55—56. — *A.* and *B.* Larvae with ten chaetigerous segments seen from the ventral side (A) and from the left side (B). Characteristic are the four pairs of tentacular cirri, the very large mouth, and the wine-red colour in the hindmost part of the intestine. — From plankton N. of Ven, depth 40 to 0 m, on $^{29}/_{8}$-1938 (drawn from life on the same day). — *C.* and *D.* Older larvae with 11 to 12 chaetigerous segments and two tentacles (C, seen from the dorsal side) and with fifteen chaetigerous segments (D, seen from the right side; with the pharynx everted). Both from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{28}/_{8}$-1938. — *E.* Old Nectochaeta from Gullmarfjord-plankton (Bohuslän, Swedish W. coast), depth 40—0 m, seen from the dorsal side. Caught and drawn from life on $^{22}/_{8}$-1945.

In our samples from the Sound the larva in question was taken off Ven on the following dates: $^{28\text{-}29}/_{8}$-38; $^{25}/_{9}$-38; $^{22}/_{12}$-38; $^{7}/_{1}$-39; $^{28}/_{1}$-39; $^{17}/_{6}$-39 (about 25 spms.); $^{2}/_{9}$-39, and $^{16}/_{9}$-39, and off Helsingør on: $^{7}/_{10}$-41 (4 Metatrochophores); $^{2}/_{12}$-41 (3 large Trochophores), and $^{4}/_{6}$-42 (11 young Trochophores). Thus this larva occurs in the summer, the autumn, and the early winter, while no larvae are present in the spring. Normally only one to three larvae are found together in a main series (10 vertical hauls). On $^{17}/_{6}$-39, however, 25 larvae in all stages of development were found. As in *Phyllodoce groenlandica*, the breeding season seems to set in very suddenly and intensively (in June), to decrease slowly towards the early winter. Only in the oldest larvae found in the plankton had the development of the tentacles commenced.

Eulalia (Eumida) sanguinea ØRSTED. Northern and middle parts of the Sound, rare.

Reproduction: A. Literature. ALLEN (1915) reports breeding from Plymouth in May-July: "eggs green, occasionally reddish". GRAVELY (1909 a) describes and figures some

Phyllodocid larvae from the Isle of Man taken in July 1907 and 1908, which, apart from the failing median tentacle, seem to agree in all essentials with *Eulalia sanguinea*, ripe specimens of which were found in the same locality together with the larvae. Nolte (1938, p. 224—25) discusses Gravely's larvae and seems to agree with him in referring them to *Eulalia sanguinea*. The *Trochophora* was 350 μ long. The *Metatrochophora* II, 650 μ long, is figured by Gravely ("Phyllodocid B"), and has four distinct pairs of tentacular cirri. The *Nectochaeta*, 1000 μ long, is not figured; the number of chaetigerous segments in this stage is not mentioned. Observations on a live *Nectochaeta* showed two pairs of tentacles, while the median tentacle characteristic of the adults could not be seen and probably had not yet developed. The intestine of the live *Nectochaeta* was green, the surrounding layer was brownish-opaque. The pygidium was darker than the other parts of the body. All stages from the *Trochophora* to the *Nectochaeta* were provided with yellow pigment spots. McIntosh (1908, monogr., p. 66) has observed young specimens in the crawling stage with 16—17 segments on the bottom in June and October, and (p. 69) ripe specimens at St. Andrews from May to August and at Plymouth from May to July.

Fig. 24. *Eulalia (Eumida) sanguinea* Ørsted. Ripe egg from a female captured in Fænø Sund, the Little Belt, depth 30 to 50 m, on $^{26}/_{7}$-1944. The female spawned when stirred. On the same day the males had vivaciously moving spermatozoa.

B. Own remarks. In Fænø Sound, the Little Belt, ripe males and females were abundant at a depth of 30—50 m on $^{26}/_{7}$-1944. The males contained vigorously moving spermatozoa, and the females spawned, when stirred, greenish-brown, globular eggs, 80 to 85 μ in diameter (fig. 24) with a very thin egg-membrane.—As already mentioned under "General remarks on Phyllodocid larvae" I think it justifiable to refer the *Nectochaeta* larvae shown in fig. 25 to the genus *Eulalia*. Judging from the size and shape of the *Nectochaeta* stage, it does not belong to the genus *Phyllodoce*, and if I am right in referring the pink Phyllodocid larvae (fig. 23) to the genus *Genetyllis* or *Notophyllum*, the present larvae must belong to the last of the Phyllodocid genera with four pairs of tentacular cirri, viz. *Eulalia*. The fact that no unpaired median tentacle (characteristic of the adult *Eulalia*) was found in the three larval specimens from the Sound is in close agreement with Gravely's observations (l. c.) on his supposed *Nectochaeta* of *Eulalia sanguinea* from the Isle of Man. It must be supposed that this median tentacle in the genus *Eulalia* is formed later than the paired tentacles.

The three *Nectochaeta* larvae, which I refer to "*Eulalia sp.*" (fig. 25), were all taken in the same plankton series off Ven, 18—0 m, on $^{1}/_{8}$-40, and were drawn when still alive on $^{2}/_{8}$-40. The smallest larva (fig. 25 A) was 630 μ long, with 8 chaetigerous segments, the two largest larvae (fig. 25 B) were 960 μ long, with 9 chaetigerous segments. The "carapace" was already much reduced, all the cilia had been lost (a remnant of the ciliary ring was, however, observed on either side of the head, but only in the largest larva), the two pairs of tentacles as well as the four pairs of tentacular cirri were well developed. Two large, black eyes, brownish-

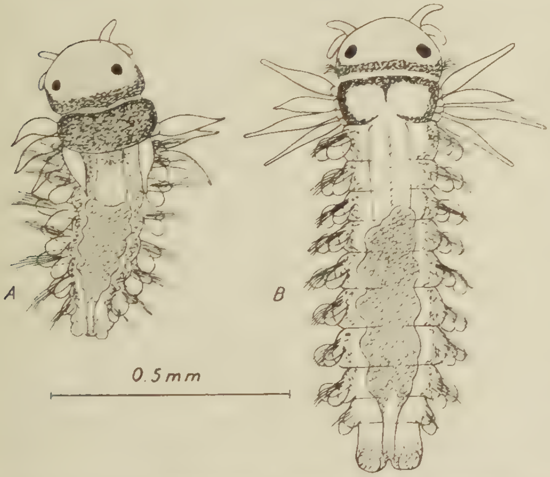


Fig. 25 A-B. *Nectochaeta* larvae probably belonging to *Eulalia viridis* (Müller) (see the text pp. 57-58). Taken in plankton off Ven, depth 18 to 0 m, on $^{1}/_{8}$-1940 (drawn from life on $^{2}/_{8}$-1940).

black pigment on the caudal margin of the prostomium and on the "carapace", light reddish-brown pigment on the front part of the prostomium and along the sides of the body. Pharynx colourless, intestine and anal segment olive-green. The yellow spots of pigment which according to GRAVELY (l. c.) are characteristic of the *Nectochaeta* of *Eulalia sanguinea*, were not found in our larva, which, therefore, should probably be referred to another species of *Eulalia*. The very pronounced dark pigmentation in our larvae possibly points to *Eulalia viridis* (see this), but nothing definite can be stated. As, however, only three larvae found on the same date are present in our four years' samples from Ven and Helsingør, the larvae must belong to a rare species, and are only of little importance in the plankton.

Eulalia (Eumida) bahusiensis BERGSTRÖM. Middle part of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Eulalia (Sige) macroceros GRUBE. Northern part of the Sound, rare.

Reproduction: A. Literature. McINTOSH (1908, monogr., p. 62) states that according to VON MARENZELLER (1874) this species had ripe females in August and dark bluish-green eggs.

B. Own remarks. Nothing is known about the development in the Sound.

Eulalia (Hypoeulalia) bilineata JOHNSTON. Middle part of the Sound, rare.

Reproduction: A. Literature. McINTOSH (1908, monogr., p. 52) states that this species is mature in May to July. Nothing is known from the Sound.

Eulalia viridis (MÜLLER). Northern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. ALLEN (1915) states about the breeding near Plymouth: "Eggs in January and February; abundant in May and June. None found at end of July or in August". HORNELL (1891) describes the eggs and Trochophores of a Phyllodocid from Jersey, which according to GRAVELY (1909 a) and NOLTE (1938, p. 221) should probably be referred to *Eulalia viridis*. The green, pear-shaped, slimy egg masses, about 20 mm across, were found in large numbers in March to April on sandy spots among the rocks. They adhered to the sand by a slimy peduncle five to seven cm long, and each egg mass contained a large number of eggs 80 μ in diameter. The Trochophores and the first *Metatrochophora* stages are described, but no older stages have been seen. MEYER (1938, pp. 334—389) describes and figures the eggs and Trochophores reared at Plymouth and near Heligoland. Main spawning in January to February; egg masses deposited on red algae, brown algae, and sponges below the low water mark, and by Heligoland on Laminarians in March to April. The egg mass, globular, slimy, 10—30 mm across, contained green ova which were 0.09 to 1.00 mm across. The larvae hatch as Trochophores after seven to ten days without having devoured the surrounding slime. Trochophores twenty days old had still no teletroch. Two *Trochophora* stages are figured. Larvae kept in large dishes died without showing any further signs of development. HOFKER (1920—22, p. CLIX) mentions (without descriptions or figures) a *Nectochaeta* of *Eulalia viridis* from plankton taken off Scheveningen (Holland) in May.

B. Own remarks. The *Metatrochophora* II and the *Nectochaeta* have never been described nor figured. The three *Eulalia* larvae (fig. 25) mentioned under *Eulalia sanguinea* (see the description of these on pp. 57—58) should most probably be referred to *E. viridis*, but no definite proof can be given.—Dr. H. BLEGVAD has kindly informed me that a female of this species taken in the western Limfjord on $^{30}/_{4}$-1932 contained a large number of eggs.

Eteone longa FABRICIUS. Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. MEEK and STORROW (1924, pp. 453—55) found ripe males and females of *Eteone arctica* (= *E. longa*) off Northumberland near the surface, drifting in the current, but . . . "maintaining their position by active contraction and wriggling movements", on $^{21-26}/_{3}$ and $^{21-27}/_{4}$-1924 at water temperatures of from 3.7° to 5° C, and "during the beginning of ebb and at a period of full moon" or at "half-ebb and just after full-moon". The ripe females were twice as large as the ripe males. "Living, and all gave evidence of being mature, were kept in a bottle of sea-water for a couple of days, and spawned, yielding a large number of eggs without an egg-capsule being formed".—WILLEMOËS-SUHM (1871, figs. 5, 6, 7 and 8) describes and figures the Trochophores and Metatrochophores of an *Eteone* (four tentacles, two pairs of tentacular cirri), which he refers to *Eteone pusilla* ØRSTED. LESCHKE (1903, pl. 7, figs. 3—5) describes and figures the *Metatrochophora* and *Nectochaeta*-larvae of a somewhat different species of *Eteone*, and he also refers his larva to *Eteone pusilla*. NOLTE (1938, p. 232) discusses the finds of WILLEMOËS-SUHM and LESCHKE, and shows that none of the larvae belong to *Eteone pusilla*, while the larvae figured have bristles on segment II (i. e. the segment caudal to that which carries the two pairs of tentacular cirri). In northern species of *Eteone* such bristles on segment II are only known from *Eteone flava* FABR., and *Eteone longa* FABR. Since, furthermore according to NOLTE (l. c.), LESCHKE's larvae belong to another species than those described by WILLEMOËS-SUHM, it seems probable that the two larval species found must be referred to *Eteone flava* and *E. longa* respectively. NOLTE (l. c.) accordingly calls the larva of WILLEMOËS-SUHM "*Eteone longa*" and those of LESCHKE "*Eteone flava*" but emphasises that he might just as well apply the names reversely.

B. Own remarks. NOLTE (l. c., p. 233) mentions twice that the larvae figured by WILLEMOËS-SUHM are schematic — "reichlich schematisiert". More astonishing is his conclusion that the larvae described by WILLEMOËS-SUHM cannot be referred to the same species as the larvae described by LESCHKE, while LESCHKE himself is of opinion that the figures of WILLEMOËS-SUHM agree well with his own larvae. NOLTE mentions the following characters, according to which they should be referred to two different species: The time at which the mouth appears; the more or less conspicuous umbrella; the pigmentation; eyes with or without lenses; the occurrence or non-occurrence of cilia on tentacles and tentacular cirri, and the shape and development of the apical ciliary tuft, — all features which cannot be figured correctly in such rough sketches as those given by WILLEMOËS-SUHM. As, moreover, both larvae are from Kiel and have all the main features in common, I have — in contradistinction to NOLTE — no hesitation in referring them to one and the same species. WILLEMOËS-SUHM further says that the larvae may occur in large numbers at the surface of the bay of Kiel, and that the larvae have only a short planktonic life. — This seems to show that the larvae are produced in the neighbourhood and by parents which are common in the area. Since *Eteone longa* and *E. flava* are the only possible parents (cf. NOLTE l. c., p. 232), and *Eteone longa* is by far the commonest in the area in question, it seems justifiable to refer the larva to this species.

The spring plankton in our main series from the Sound contains several larvae of *Eteone* all belonging to the same species and agreeing very well with the figures of WILLEMOËS-SUHM and LESCHKE. The *Metatrochophora* II from the Sound (fig. 26 A) seems thus to be a somewhat older stage than LESCHKE's pl. 7 fig. 4 and is also rather similar to the Metatrochophores of WILLEMOËS-SUHM, l. c., figs. 7 and 8. The larvae from the Sound have two pairs of claret-red eyes and are provided with grass-green spots of pigment. The tentacles are, however, much earlier developed in the larvae of WILLEMOËS-SUHM than in those from the Sound. In the stage with four to five chaetigerous segments the latter have a distinct prototroch, but no tentacular cirri are developed, and the tentacles have not yet appeared. The larva, 460 μ long, has dark-greenish pigment on the prostomium, on the base of the prototroch, and on the anal segment. The contents of the intestine are greyish-brown, dark brown nearest the anal opening. Otherwise the animal is colourless apart from the wine-red eyes. The *Nectochaeta* stage (fig. 26 B and E), somewhat older than that figured in pl. 7, fig. 5 by Leschke, is actually no pelagic stage, and larvae in this stage, which have only 6 to 7 chaetigerous segments, will, if taken from the plankton and examined in a Petri dish, at once seek to the bottom, where they will crawl about and form a slimy tube. This *Nectochaeta* stage, 905 μ long, has accordingly all the characteristics of the adults. The four distinct colourless tentacles and the two pairs of tentacular cirri are well developed. On the boundary between the prostomium and the peristomium a colourless bud is seen on each side. It does not seem to develop into a tentacular cirrus. The failing dorsal cirrus on segment II is a typical *Eteone*-character, and the presence of bristles on the same segment proves that the larva belongs either to *Eteone flava* or to *E. longa*. The green

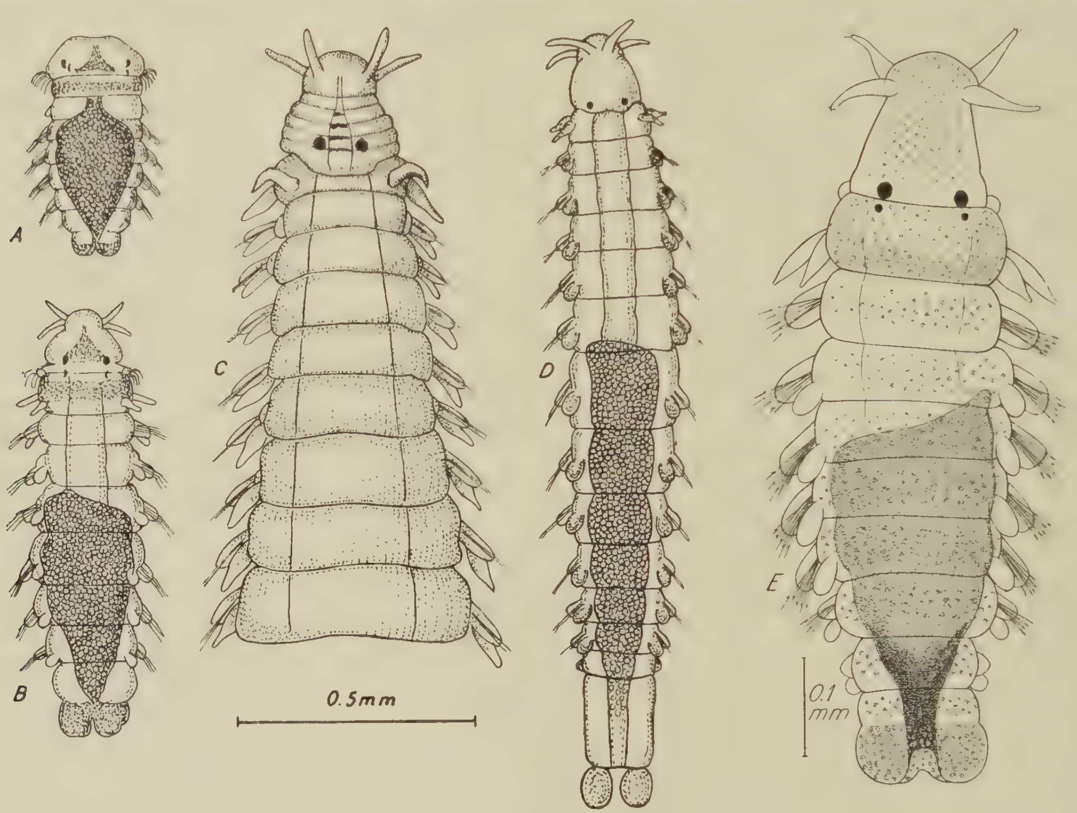


Fig. 26 A-E. *Eteone longa* Fabr. — *A* and *B*. Larvae from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{12}/_{3}$-1938. — *A*. *Metatrochophora* II. — *B*. *Nectochaeta* (both seen from the dorsal side). — *C*. Front part of bottom stage with about 60 chaetigerous segments, detritus sampler off Ven, depth 4 m, sandy bottom, caught and drawn from life on $^{12}/_{8}$-1938. — *D*. Young, metamorphosed bottom stage seen from the dorsal side; from a bottle collector exposed off Ven, depth 16 m, from $^{27}/_{5}$- to $^{19}/_{7}$-1941 (drawn from life on the latter date). — *E*. Old *Nectochaeta* (oldest planktonic stage known, "svimming-crawling stage") from plankton off Snekkersten, depth 8 to 0 m, taken on $^{3}/_{4}$-1945 (drawn from life on $^{4}/_{4}$).

pigment on the prostomium, on segment I, and on the anal segment, already mentioned from the *Metatrochophora* II, as well as the two pairs of claret-coloured eyes are still present in the *Nectochaeta*, which has greenish spots of pigment also over the other segments of the body. The contents of the intestine are greyish-brown. The prototroch is much less prominent, or totally reduced, and just in front of this is a bundle of larval bristles on each side. — Larvae of this type were found in our four-year-samples from Ven taken on the following dates: $^{12}/_{3}$-38 (56 spms.); $^{3}/_{4}$-38 (6 spms.); $^{18}/_{4}$-38 (1 spm.), and $^{10}/_{4}$-39 (5 spms.), and off Helsingør on $^{15}/_{5}$-42 (12 spms. in all stages); $^{20}/_{6}$-42 (2 spms.), and $^{3}/_{4}$-45 (2 spms., cf. fig. 26 E). The time of their occurrence in the plankton is thus very limited, a fact which seems to agree very well with their pelagic development. Their main occurrence in March-April and May is also in good agreement with an observation kindly placed at my disposal by stud. mag. Erik Rasmussen, viz. that a specimen of *Eteone longa* from Frederikssund in Roskilde Fjord, placed in an aquarium in March 1943, spawned eggs in irregular slimy lumps. — By far the largest number of pelagic larvae found were older larvae able to crawl; thus the development in the pelagic stage seems to be very rapid. — We succeeded in observing the larvae in the young bottom-stages also. In a bottle collector exposed at a depth of 16 m off Ven from $^{27}/_{5}$ to $^{19}/_{7}$-41 a single bottom stage was found (fig. 26 D), which was referred without difficulty to the same species. This specimen, 1430 μ long, had eleven chaetigerous segments, the smallest of the two pairs of claret-red eyes had now disappeared, the contents of the intestine were yellowish-brown, but the tentacles, the tentacular cirri, and the dorsal cirri agreed closely with those of the *Nectochaeta*. A faintly greenish pigmentation was still seen, especially on the prostomium and the anal segment. A haul with the detritus sampler of Mortensen off Ven, depth 4 m, purely sandy bottom, $^{12}/_{8}$-38, yielded a bottom stage with about 60 chaetigerous segments which was sketched in a living state (fig. 26 C). This stage also showed so close similarity to the youngest bottom stage found that they should be referred to the same species, and the dorsal cirri in the 60-segmented specimen showed very clearly that the species was *Eteone longa*, which is also the commonest species of *Eteone* in the Sound.

In the harbour of Copenhagen, however, Erik Smidt (1944, p. 253, fig. 4 A) took a larva on $^{6}/_{6}$-39, which — though only roughly sketched — bears some resemblance to the larvae of Willemoës-Suhm and Leschke and to those from the Sound. The larva from Copenhagen was green-pigmented, had two large and two small eyes, four tentacles, only one pair of tentacular cirri, and four chaetigerous segments, thus being in a stage of development intermediate between those shown in figs. 7 and 8 of Willemoës-Suhm.

Eteone flava Fabricius. Middle part of the Sound, rare.

Reproduction: See the remarks under *Eteone longa*.

Eteone spetzbergensis Malmgren. Northern part of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Eteone (Hypereteone) lactea (= E. pusilla). Middle and northern parts of the Sound, rare.

Reproduction: A. Literature. The larvae, which were referred to this species by Willemoës-Suhm (1871) and Leschke (1903), may, according to Nolte (1938), belong either to *Eteone flava* or to *Eteone longa*. See the remarks under the latter species.

B. Own remarks. Nothing is known from the Sound.

Eteone (Mysta) barbata MALMGREN. Middle and northern parts of the Sound, rather common.

Reproduction: A. Literature. Unknown.

B. Own remarks. In the winter main-series taken off Helsingør small larval Phyllodocids were present in large numbers on $^{2}/_{12}$-41 (30 larvae in all stages); $^{19}/_{12}$-41 (195 larvae in all stages); $^{3}/_{1}$-42 (38 Nectochaetes); $^{31}/_{1}$-42 (3 Nectochaetes), and $^{5}/_{9}$-42 (4 Nectochaetes). These larvae (fig. 27 A-B) showed the following features: *Metatrochophora* II, 560 μ long, somewhat hunchbacked with five chaetigerous segments, two budding tentacles, two pairs of sealing-wax-red eyes, a prototroch, and two broad tentacular cirri on each side. The prostomium has the vaulted appearance typical of the umbrella of Phyllodocid larvae. The *Nectochaeta* (fig. 27 B, 480 μ long) is smaller, in length as well as in breadth, than the *Metatrochophora* II. This fact was observed on large numbers of larvae and seems to be connected with the lecithotrophic mode of feeding of this larva (cf. pp. 436—438). Six chaetigerous segments, all, except the first, with dorsal as well as ventral cirri. Two pairs of tentacular cirri, two anal cirri somewhat longer than in the preceding stage. The prostomium has been much reduced in size from that of the *Metatrochophora*, and two tentacles have commenced to appear. Two pairs of red eyes. The intestine has greyish-green contents, changing in the caudal section into a yellowish-red intestine with brownish black contents. No traces of a prototroch are seen. — In the main-series from Ven these larvae, apart from a few specimens which may have been overlooked, never occurred in large numbers. The two pairs of tentacular cirri point to the genus *Eteone*, and, if it belongs to this genus, the species must be referred to *Eteone flava*, owing to the bristles on segment II, for the larva of *Eteone longa* has already been identified. The larvae in question seem, however, to differ so much from those of *Eteone longa* that they can hardly be referred to the closely related species *E. flava*, which is moreover rare in the Sound, while the larvae in question are common (up to 800 larvae were taken in a water column covering 1 sq.m of bottom!). The only Eteonid apart from *Eteone longa*, however, which is of fairly common occurrence in the Sound is *Mysta barbata*. As the adults of this species, like those of *Eteone longa* and *E. flava*, have bristles on segment II, the larvae in question may just as well be referred to *Eteone (Mysta) barbata*. This seems to be supported by the following facts: the larvae seem to be restricted to the northern part of the Sound, where the adult *Mysta barbata* also has its main occurrence. Further, *Mysta barbata* is restricted to the Hypobath-region of the Sound, i. e. similarly to the other species living here it must be expected to breed late in the autumn, which is in good agreement with the larval maximum in December. — It seems most reasonable, therefore, to refer the larvae to *Mysta barbata*, but no definite proof can be given.

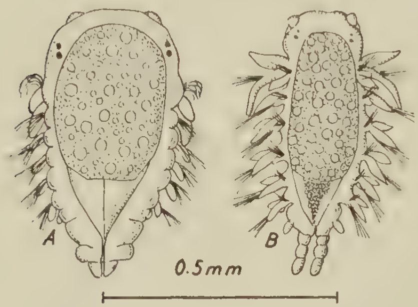


Fig. 27 A-B. Larvae probably belonging to *Eteone (Mysta) barbata* MALMGREN. From plankton between Hellebæk and Kulla Gunnarstorp, depth 30 to 0 m, drawn from life on the day of capture. — *A. Metatrochophora* II, seen from the dorsal side (caught on $^{2}/_{12}$-1941). — *B. Nectochaeta*, seen from the dorsal side (caught on $^{19}/_{12}$-1941).

Mystides sp. The adult stage unknown from the Sound.

Reproduction: A. Literature. GRAVELY (1909 a) describes and figures as "Phyllodocid A" from Port Erin plankton a Phyllodocid larva with four tentacles and three pairs of tentacular cirri distributed over two segments, a fact which at once refers it to the genus

Mystides. The Metatrochophores are not figured, but the *Nectochaeta*, 800 μ in length in a fixed state, shows clearly the four tentacles and the three pairs of tentacular cirri distributed over two segments. The *Metatrochophora* II has still two pairs of eyes, the *Nectochaeta*, however, one pair only. NOLTE (1938) discusses some of the points in GRAVELY's description (l. c.). —ALLEN (1915, p. 618) records from Plymouth a "female with dark green eggs in May" of the species *Mystides limbata.*

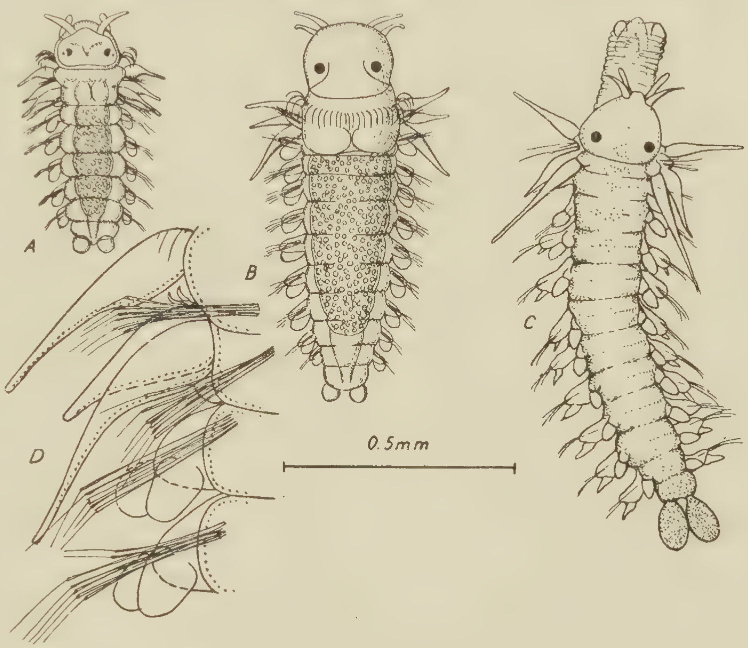


Fig. 28 A-D. *Mystides sp.* Larvae from plankton.—*A.* Transitional stage between *Metatrochophora* II and *Nectochaeta*, from surface plankton off Frederikshavn, NW. Kattegat, caught and drawn from life on $^{25}/_{7}$-1939.—*B. Nectochaeta* with ten chaetigerous segments, from plankton off Frederikshavn, depth 6 to 8 m, caught and drawn from life on $^{31}/_{7}$-1939.—*C. Nectochaeta* with 11 chaetigerous segments (the pharynx is extended) from plankton off Helsingør taken and drawn dead on $^{11}/_{11}$-1941.—*D.* The first four chaetigerous segments of the larva fig. *A* at larger magnification.

B. Own remarks. A main series from Helsingør taken on $^{11}/_{11}$-41 contained a single *Nectochaeta* larva (fig. 28 C) with 11 chaetigerous segments, about 900 μ long, with two black eyes and four tentacles on the inversely heart-shaped prostomium, and three pairs of tentacular cirri distinctly distributed over two segments, i. e. all the characteristics of the adult *Mystides* and of the *Mystides* larva described by GRAVELY (l. c.) and discussed by NOLTE (l. c.). This is the only find from the Sound. From Frederikshavn, NW. Kattegat, two further larval stages are at hand, which may serve as a supplement. The small one (fig. 28 A and D), taken in surface plankton on $^{25}/_{7}$-39, measures 490 μ in length, has 7 chaetigerous segments and two pairs of eyes (as the *Metatrochophora* II described by GRAVELY). It seems to form a transitional stage between the *Metatrochophora* II and the *Nectochaeta.* Thus the four tentacles are well developed, and so are the three pairs of tentacular cirri distinctly distributed over two segments, but the prototroch is still very active with long cilia. Here, also, the prostomium is inversely heartshaped with a V-shaped greyish-green pigmentation on the dorsal side. The next stage (fig. 28 B), taken in plankton at a depth of 6–8 m on $^{31}/_{7}$-39, is 780 μ long, has ten pairs of chaetigerous segments, four tentacles, three pairs of tentacular cirri on two segments, and two eyes; the prototroch seems still to be rather active. Both these stages were colourless with a greyish-green front part and a greyish-brown rear part of the intestine. These three stages, so different in size, but so similar in organisation, and all with three pairs of tentacular cirri distributed over two segments, seem to show such a certain character and to agree so well with the "*Mystides*" larva of GRAVELY (l. c.) that they must belong to *Mystides*, probably even to the same species, which seems to be rather common in the NW. Kattegat but extremely rare in the Sound. Two species of *Mystides* may be expected to occur in Danish waters, viz. *M. augeneri* known from the "*Amphioxus* bottom" off Heligoland, and *M. borealis*, known from Arctic seas and onwards to the British Isles and Madeira. So far, however, no adult specimens of the genus *Mystides* are known from our seas.

Tomopteris helgolandica Greeff. A plankton haul taken off Hellebæk—Kulla Gunnarstorp, 30—0 m, on $^7/_{10}$-1941 yielded an adult specimen of *Tomopteris helgolandica* (determined by Mrs. E. Wesenberg-Lund). In a plankton haul from the same depth and the same locality, taken on $^{19}/_{12}$-41, one more adult specimen was found. When discovered in our plankton bottles the day after the capture, both specimens were already in dissolution and were not, therefore, fixed.

Reproduction: A. Literature. Carpenter and Claparède (1860), Meyer (1890), Flattely (1923), and Apstein (1916) have described the young planktonic stages of this pelagic Annelid. Even the youngest stage found, 380 μ long, with a prototroch, one pair of budding tentacles, and three pairs of distinct parapodia without chaeta, shows clearly that the larva is a Tomopterid, and the older larvae are nearly as easily recognisable as the adults.

B. Own remarks. No observations on this species are known from the Sound.

Nereis pelagica Linné. Middle and northern parts of the Sound, common.

Reproduction: A. Literature. Herpin (1925) has described the development and figured the larval stages from Cherbourgh. His investigations can be summarised as follows: Spawning only in December to January by epitoquous specimens (also a summer spawning is, however, recorded from other seas). Judging from its northern distribution the species probably spawns in shallow water in the winter and in deep water in the summer. The unfertilised egg is 170 μ across, and the eggs are shed freely in the water. The larvae hatch seven days after fertilisation with all cilia reduced, and have no pelagic stage, but at once commence their crawling life on the bottom. "Dépit de son nom, *Nereis pelagica* ne possède pas de larve pelagique". The hatching larvae have small buds, indicating the future tentacles, tentacular cirri, and anal cirri; the subsequent development is very slow. A larva 28 days old had four chaetigerous segments only, a larva 83 days old was less advanced in development than a *Perinereis marioni* in the hatching stage. "En resumé, la larve de *N. pelagica* se charactérise par son unique couronne ciliaire, la brièvité de ses appendices, la longueur des arêtes de ses soies et l'extrème lenteur de son dévelopment". Several fine figures of developing larvae are given. — Wilson (1932a) describes and figures the development from Plymouth. His observations are as follows: *Heteronereis* specimens spawned in plunger jars, in which the development was completed. The undeveloped egg was 180 μ across, and the eggs were pelagic. Fertilisation on February 4th; the larvae hatched $3^1/_2$ days later and commenced the pelagic life, which may last until 18 days after fertilisation. Beautiful figures of all stages of developing larvae until the crawling stage. — The larva described and figured by Leschke (1903, pl. 7 fig. 8) and by him referred to *Nereis dumerilii* (see this) should likewise be referred to *Nereis pelagica*. - Sæmundsson (1918, p. 200) found epitoquous specimens near Iceland in April—May and in October. Nordgaard (1912) observed a pelagic female spawning swarms of eggs (190 μ across) near Bergen in August.

B. Own remarks. The investigations made by Herpin and Wilson came to quite different results. In both cases the material was derived from the Channel, and both investigations were made in the winter. But while the larvae of Herpin are non-pelagic and rather large when hatching, Wilson's larvae hatch in a much younger stage and commence a pelagic life. Thus this species is able to vary its mode of development to an amazing extent.

In spite of this variation, however, the larvae shown in WILSON's and HERPIN's drawings are very similar. The ciliation is, of course, well developed in the pelagic form and entirely absent in the crawling form, but the shape of the two larval forms is nearly the same and is quite different from that of the broad, hunch-backed, yolky, atoquous larvae of *Nereis diversicolor, N. dumerilii,* and *N. caudata.* — The larvae of *Nereis pelagica* are, therefore, easily distinguishable from those of *N. diversicolor* and *N. dumerilii*, the only other two Nereids which are fairly abundant in the Sound. — During the four years' investigations only two larvae were present in the plankton which can be referred to *Nereis pelagica* (fig. 29). Both these larvae are Nectochaetes, with four chaetigerous segments, closely similar to those figured by WILSON (l. c. fig. 6), but without the slightest trace of such bands of cilia as are found in WILSON's larvae. Our larvae were taken in plankton off Ven on $^{12}/_{11}$-38, i. e. in the winter (which was also the case by Cherbourgh and Plymouth), and off Helsingør on $^{4}/_{6}$-42 (at the height of summer). Dr. H. BLEGVAD, however, observed epitoquous specimens of this species off Sletterhage on $^{12}/_{4}$-30 and off Sejrø on $^{13}/_{4}$-30, and has kindly allowed me to mention his finds. The non-ciliated appearance of the two larvae found, and the fact that these are the only finds of planktonic larvae of a species the adult stages of which are very common in the Sound, seem to show that the species will normally develop here in a non-pelagic way, as was also the case at Cherbourgh. The highly varied development of this and other Nereids makes it probable that in especially favourable years the species will reproduce by pelagic larvae even in the Sound.

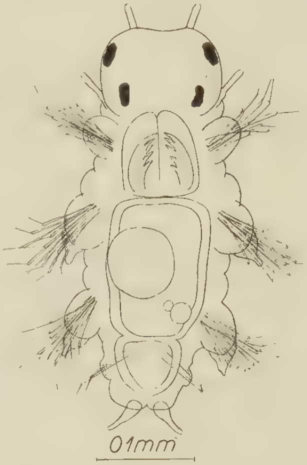


Fig. 29. *Nereis pelagica* LINNÉ. *Nectochaeta* larva from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{12}/_{11}$-1938. Seen from the dorsal side.

Nereis diversicolor MÜLLER. Extremely common throughout the Sound, especially in Baltic water.

Reproduction: A. Literature. HERPIN (1925) gives the following data: *N. diversicolor* spawns at Cherbourgh the whole year round. The species is atoquous. The eggs, spawned through ruptures of the body wall, are 230 μ across. The young stages of development are not known. "On ignore si la larve passe par une phase pélagique". The egg is figured, but no figures are given of the larva. McINTOSH (1907) states that the spawning maximum at St. Andrews is in March, and he figures and describes the young bottom stages. The youngest bottom stage observed had three chaetigerous segments, two tentacles, two palps, and one pair of tentacular cirri. The eyes still consisted of scattered spots of pigment. The shape was broader than that of the *N. pelagica* larva, and the stomach contained quantities of yolk, among which rather large grains of fat occurred. Such post-larvae were found in the tubes of the adults, and in May several free eggs were observed among mud particles in the walls of these tubes. It is not known whether these bottom stages were preceded by a pelagic stage. — HOFKER (1930, p. 199—201) describes and figures some larvae from the Zuidersee which he refers to *Nereis diversicolor*, since "the setae of the Nectochaetes closely resemble those of *N. diversicolor*, which species is also the most frequent in the southern Zuidersee" (translated from the German). In the same paper, however, HOFKER (l. c. p. 194) states that larvae of *Nereis succinea* and *N. dumerilii* might be expected to occur within the area in question. — HOFKER's larvae, which were rather common in plankton in July-August, comprised: Trochophores (140 μ long) and Metatrochophores (127 to 140 μ long), both rather rare; four-segmented Nectochaetes (175 μ long), common, with two (four?) eyes, two tentacles, two tentacular cirri, two anal cirri, and a distinct prototroch; and finally older Nectochaetes (390 μ long), less common, with seven segments, two red pigment spots on the prostomium, cilia at the base of each parapodium, prototroch, and a well developed oesophagus with jaws. The size of these larvae up to the four-setiger stage, viz. 127 to 175 μ, does not agree at all with the egg size, 320 μ, stated by HERPIN (l. c.). Accordingly *Nereis diversicolor* must be able to vary its egg size and mode of development from place to place (as known for some other Nereids), or the larvae described by HOEKER should be referred to one of the other Nereids occurring in the Zuidersee, e. g. *Nereis dumerilii* or *N. succinea*. HERPIN (l. c.) as well as McINTOSH doubt the statement given by MAX SCHULTZE (1856) that the species is hermaphroditic and viviparous in the Baltic. Owing to the great lability in the mode of reproduction so well known in Nereids in connection with the special brackish water conditions in the Baltic it is possible that SCHULTZE's observation is correct. – THAMDRUP (1935, p. 35) found ripe specimens at Skallingen from the middle of March to April (July).

B. Own remarks. The few larvae of *Nereis pelagica* mentioned above are the only specimens of slender *Nereis* larvae known from our plankton investigations. All the other *Nereis* larvae found in our samples belong to the broad form, which is referred to as the "nereidogene larval type" (e. g. by HEMPELMANN 1911). They are broad, hunch-backed, and distended by large amounts of yolk. Among the Nereid forms from the Sound such larval types are only known for *Nereis diversicolor* and *Nereis dumerilii*, of which *N. diversicolor* is by far the commonest adult species. The "nereidogene larvae" of the Sound plankton should therefore be referred either to one of these forms or to both of them. — A small, nereidogene *Nereis* larva with three to four chaetigerous segments is very common in the Sound plankton (fig. 30). It agrees well with HERPIN's figures of the *Nereis caudata* larva (1925, fig 48), and still more closely with his youngest stage of the *Nereis dumerilii* larva (HERPIN 1925, fig 69). Thus, it seems tempting to identify our Sound-larvae with the *Nereis dumerilii* larva, which, however, on closer examination proved to be four times as long as our larvae from the Sound. The following table will show the sizes of eggs and larvae of *Nereis pelagica*, *N. diversicolor*, and *N. dumerilii*.

Our nereidogene larvae from the Sound measure 360 to 450 μ in length. They are accordingly too large to be referred to *Nereis pelagica*, the shape of which is also quite different, and they are far too small to be referred to *Nereis dumerilii*. Since, moreover, 1) the egg-size of *N. diversicolor* is intermediate between those of *N. pelagica* and *N. dumerilii* in the nereidogene stage and quite theoretically point to a four-segmented larva about 400 μ in length, 2) such larvae are very common in the plankton, 3) the adult *Nereis diversicolor* is by far the dominant species of *Nereis* in the Sound, and 4) the pelagic larval stage of *N. diversicolor* has hitherto been unknown, it seems justifiable to refer the larvae found to this species. The breeding season (the larvae occur in the Sound in the spring) is likewise in good agreement

Species	Egg size, diameter	Total length of larva with four chaetigerous segments
Nereis pelagica	170 to 180 μ	220 to 250 μ (HERPIN 1925, fig. 37—39)
Nereis diversicolor	230 μ	?
Nereis dumerilii: nereidogene form	400 μ	1580 μ (HERPIN 1925, fig. 69)

with the occurrence of the adults in shallow water, while "deep water" species in the Sound will spawn in the autumn. The fact that this larval form is also common in the harbour of Copenhagen (Erik Smidt 1944), where *Nereis diversicolor* is still more dominant than in the Sound itself, seems likewise to support the determination. — In spite of its pelagic occurrence this young larval stage of *Nereis diversicolor* (fig. 30) is an absolutely nereidogene type. All the specimens found in the plankton are of about the same size, the growth of the pelagic stage is rather slow, all the larvae found were in the stage with three or four chaetigerous segments, and the large mass of yolk in the intestine shows that the larvae will not take any food from the plankton, but will obtain their nourishment from the yolk contained in the egg. The small remnants of the prototroch still present will allow the larva to move slowly through the water.—Our larvae differ fairly much from those which Hofker (l. c.) refers to this species. His larvae, which are of a much smaller order of magnitude than the eggs measured by Herpin (l. c.), are also much smaller than our larvae from the Sound; thus Hofker's four-setiger stages measure 175 μ, while four setiger stages from the Sound measure 360 to 430 μ; and while our larvae are hunch-backed and lecithotrophic, Hofker's larvae seem to be of the "planktogene" type known for pelagic larvae of *Nereis dumerilii* and *N. pelagica*. It seems, therefore, impossible at present to determine the identity of Hofker's larvae. — The pelagic phase in the Sound will promote the distribution of the species; this is an advantage, but the larvae in question do not depend on the plankton as a source of food.— In our four years' samples such larvae were taken off Ven on the following dates: $^{23}/_{5}$-37; $^{6}/_{6}$-37 (30 spms.); $^{3}/_{4}$-38; $^{10}/_{5}$-38; $^{22}/_{5}$-38 (31 spms.); $^{6}/_{6}$-38 (37 spms.); $^{18}/_{6}$-38; $^{25}/_{3}$-39 (55 spms.); $^{10}/_{4}$-39 (90 spms.); $^{30}/_{4}$-39; $^{17}/_{5}$-39; $^{4}/_{6}$-39; $^{17}/_{6}$-39, and $^{3}/_{7}$-39, and off Helsingør on: $^{27}/_{4}$-42 (2 spms.); $^{15}/_{5}$-42 (about 295 spms.); $^{4}/_{6}$-42 (37 spms.); $^{20}/_{6}$-42 (27 spms.); $^{18}/_{7}$-42 (24 spms.), and $^{18}/_{8}$-42 (1 spm.); thus the season lasts from the end of March to July-August with the maximum occurrence in March-May. This is in good agreement with an observation made by Dr. H. Blegvad, who on $^{9}/_{4}$-24 at Nyborg (Great Belt) saw a female with the parapodia distended by yellow, ripe eggs. Young bottom stages like those described by McIntosh (see above) have also been found in the plankton in the Sound. On $^{24}/_{9}$-38 four such larvae were secured. They had five chaetigerous segments, had two pairs of eyes, belonged to a stage intermediate between figures B and C of McIntosh (l. c.), and did not show the slightest trace of cilia.

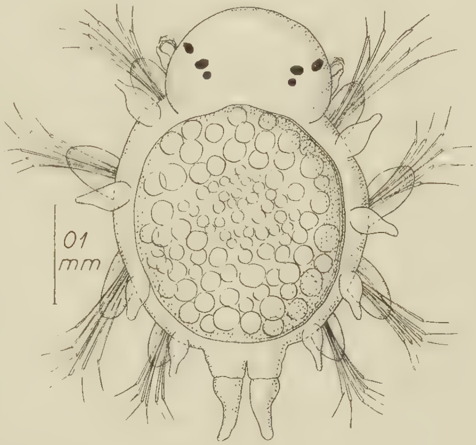


Fig. 30. *Nereis diversicolor* Müller. Lecithotrophic larva from plankton off Ven, depth 18 to 0 m, taken on $^{25}/_{3}$-1939 (drawn from life on $^{26}/_{3}$-1939); seen from the dorsal side.

Nereis dumerilii Aud. and Edw. Northern part of the Sound, not uncommon.

Reproduction: A. Literature. Only a few facts from the large literature dealing with this species will be mentioned here. The main work of Hempelmann (1911) describes the two main types of reproduction, viz. 1) Reproduction by non-pelagic "nereidogene" larvae originating from atoquous parents, and 2) Reproduction by pelagic "planktogene", larvae originating from epitoquous parents. The "nereidogene" larval type figured by Hempelmann (l. c., p. 16, fig. 1) and by Herpin (1925, figs. 69—70) corresponds rather closely to the young bottom stages of *Nereis diversicolor* figured by McIntosh (1907, fig. A—B), but the two pairs of eyes in *Nereis dumerilii* are much larger and better developed than in *N. diversicolor*. The "planktogene" larval type figured by Hempelmann (p. 31, fig. 7a—b) has the same shape and structure as the pelagic larvae of *Nereis pelagica* (Wilson 1932a, fig. 6—7), but the two pairs of eyes are larger and more distinct in *N. dumerilii*, which has no trace of the large spots of pigment so commonly found on the front part of the *pelagica*-head. Georgevitch (1938) describes, from Adria, the pelagic larvae of another *Heteronereis*-form of *N. dumerilii* originating from larger eggs than those described by Hempelmann. Georgevitch's figures are, however, too bad to be used for the purpose of identification of the larvae found in the plankton. The larvae which are referred by Leschke (1903, pl. 7, fig. 6—8) to *N. dumerilii*, seem to belong to *Nereis pelagica*.

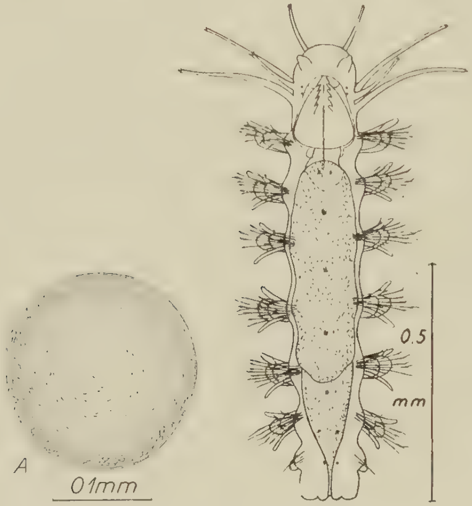


Fig. 31 A-B. *Nereis dumerilii* Aud. & Edw. — *A*. Ripe egg taken from adult female (quite distended by eggs) off Hellebæk, depth 35 m, on $^{12}/_{9}$-1941 (the egg dissected out and drawn on $^{13}/_{9}$-41). — *B*. Young bottom stage, presumably belonging to this species; seen from the ventral side (see the text p. 68). From a bottle-collector exposed off Ven, depth 16 m, from $^{24}/_{7}$ to $^{12}/_{8}$-1940.

B. Own remarks. Not a single larva present in our four years' samples can be referred to *Nereis dumerilii*. As the adults are so abundant in the Sound that their larvae might be expected to occur in the plankton, if they are pelagic at all, *Nereis dumerilii* may be supposed to reproduce by "nereidogene", non-pelagic larvae in the Sound. — Off Hellebæk, 35 m depth, an adult male and a female of this species were taken on $^{19}/_{9}$-41 (determination careful, on the basis of jaws and paragnathae). The female, of a strong yellowish-green colour, was much distended by apparently quite ripe eggs (190—200 μ across, with a very thin egg membrane, fig. 31 A). The male specimen was filled with ripe, active sperms. These observations of both sexes seem to indicate that the spawning was about to take place, and the egg size — much smaller than that which according to Herpin leads to a nereidogene larval development near France (cf. the remarks under *N. diversicolor*) — seems to point to a pelagic development. However, in the plankton of our four years' main series not a single larval Nereid was taken in the autumn samples! As moreover the adults are so frequent in the Sound that the larvae, when pelagic, must be rather common in our plankton, it seems most reasonable to conclude that in spite of their rather small eggs the larvae will develop in a non-pelagic way — probably a new mode of "nereidogene" development which may be added to the many different modes of reproduction already known in this species. — A bottle collector exposed off Ven at 16 m depth from $^{24}/_{7}$ to $^{12}/_{8}$-40 contained a young bottom stage of a Nereid (fig. 31 B) with 7 chaetigerous segments, four black eyes, and a few, small yellow spots of pigment along the back. The very long tentacular cirri already developed in that specimen agreed with the bottom stage of *Nereis dumerilii* described in Herpin's paper (1925, fig. 71), whereas the seven-segmented bottom stages of *N. pelagica* and *N. diversicolor* have much shorter tentacular cirri. Hempelmann's sketch (1911, p. 32, fig. 8 B) of the oldest "planktogene" larval stage of *Nereis dumerilii* is also very similar to our specimen from the Sound. Hempelmann's specimens, however, have larger eyes, and bristles at the base of the tentacular cirrus III. The lack of anal cirri in the specimen from the Sound is probably due to injury. In spite of the differences pointed out here, I think that our young bottom stage should most likely be referred to *Nereis dumerilii*.

Nereis virens M. Sars. One large specimen, about 25 cm long, off Hellebæk, 15 m depth, sandy bottom with *Venus* and *Mactra*, on $^{17}/_{7}$-42. One young specimen, taken in the northern part of the Sound in the summer of 1941, depth unknown.

Reproduction: A. Literature. McIntosh (1910, monogr., p. 334) has published the following observations on this species: in specimens secured in May "the females discharged from the broken surfaces (posterior) a cloud of grass-green ova", 0.03 to 0.02 mm across, i. e. very small. The same author writes: "In October the small ova occur in masses at the basis of the feet, extending into the lamellae". In the same month McIntosh observed, in the bottom tow nets, numerous faintly yellow or greenish-yellow larvae in the *Trochophora* stage, which had a diameter of 0.228 mm, e. g. a *Trochophora*-size, which seems rather large, provided that the egg sizes given above refer to ripe eggs. As nothing is stated about the identity of these larvae, and as the description of them given by McIntosh (without figures) is far from exhaustive, it cannot be decided whether or not they belong to *Nereis virens*. At a meeting held at the Zoologiska Institutionen, Lund, in the autumn of 1943 Dr. G. Gustafson, Kristineberg, gave an account of the reproduction and development of this species. His results have not yet been published, but he has kindly allowed me to mention that the development is non-pelagic.

B. Own remarks. Nothing is known about the reproduction of this species in the Sound.

Leptonereis glauca Clap. A single adult specimen of this species was taken between Lappegrunden and Hittarp in the northern part of the Sound, 30—35 m depth, on $^{31}/_{7}$-41 (E. Wesenberg-Lund det.).

Reproduction: A. Literature. The Heteronereid specimens are described by Herpin (1925) and Gravier & Dantan (1925). The breeding habits have been observed and described by Herpin (1927) as follows: The Heteronereid males with three distinctly different sections of the body swarm in large numbers at the surface of the water. The swarming seems, however, to take place after the emission of the sperms. The Heteronereid females, differing only slightly from the atoquous females, are rarely met with swarming in the water, but even such pelagic females will spawn their eggs, 240 μ across, in their tubes, where the female will aërate the developing embryos by undulating movements. The eggs are deposited in two rows and were not observed later, but Herpin is of opinion that the embryos have a non-pelagic development. —A male placed in the same aquaria as the spawning female was apparently killed and partly devoured by the female.

B. Own remarks. The female recorded here from the Sound was quite distended with apparently ripe eggs.

Nephthys ciliata Müller. Extremely common in the northern and middle parts of the Sound.

Reproduction: A. Literature. Nothing is known about the reproduction and development of *Nephthys ciliata*, whereas several observations of other species of *Nephthys* are at hand. Good figures of older planktonic *Nephthys*-larvae are given by Claparède and Metschnikoff (1869, pl. 14, fig. 3), by Häcker (1897, fig. 5), and by Fewkes (1883, pl. 4, fig. 1—12), all agreeing in a number of common features. Thus for instance the shape is slender, conical, the ciliation is restricted to the prototroch and the teletroch (the larva is exotrochous). The pharynx is large, often with distinct jaws, the anal segment has a pigmentation different from that of the body, and the contents of the intestine are of a deep verdigris or navy-blue colour. This latter characteristic feature makes the larvae easily distinguishable from most other genera in the plankton (the *Capitella* larvae may, however, have a somewhat similar colour).

B. Own remarks. Eggs shed in aquaria by a female taken in Vellerup Vig (in the Isefjord) on $^{23}/_{7}$-43 measured 120 μ in diameter, of which the egg membrane alone constituted 2—3 μ (observations by stud. mag. Erik Rasmussen). — Two different species of *Nephthys* larvae occur in the Sound plankton: one of them is common, whereas the other species has only been found in a single main series during our four years' investigations. Unfortunately we have had no opportunity to observe the metamorphosis from the pelagic life to the bottom stage, but several facts seem to show that the commonest *Nephthys* larva in our samples should be referred to *Nephthys ciliata*, which in the adult stage is the commonest Polychaete in the Sound (cf. Eliason 1920), thriving in Baltic water as well as in Kattegat water. The other species of *Nephthys* are rather rare in the Sound. Further, *Nephthys ciliata* is common throughout the Sound as far as Copenhagen, while the other species of *Nephthys* are restricted to the areas north of Ven. Since larvae of the type referred by us to *Nephthys ciliata* have been described and figured from the Copenhagen harbour also (northern as well as middle parts of the harbour, cf. Erik Smidt 1944, p. 255—256, fig. 6) whence only *N. ciliata* is known in the adult stage, as, moreover, the larvae in question are more frequent in our samples than might be expected if they belonged to one of the other species of *Nephthys*, and as the frequent occurrence of young Trochophores proves that several of the larvae originate from the Sound or its nearest surroundings, it seems justifiable to refer the larvae to *Nephthys ciliata* without further hesitation.

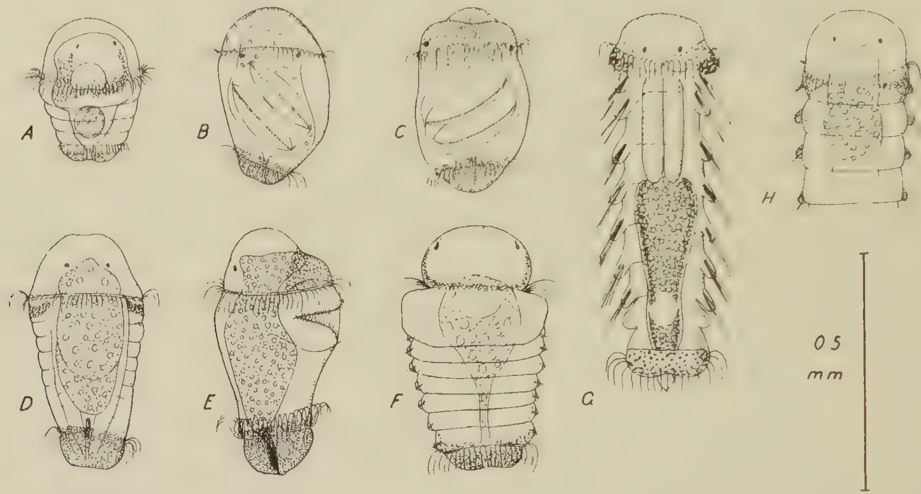


Fig. 32 A-H. *Nephthys ciliata* Müller. Larvae from plankton, all drawn from life. — *A*. Youngest *Trochophora* seen (off Ven, $^{12}/_{8}$-1940). — *B* and *C*. Trochophores with large specimens of *Coscinodiscus* in their stomachs (between Hellebæk and Kulla Gunnarstorp, depth 30 to 0 m, $^{3}/_{1}$-1942). — *D* and *E*. *Metatrochophora* I, from the dorsal side (D) and from the right side (E), (between Hellebæk and Kulla Gunnarstorp, $^{3}/_{1}$-42). — *F*. *Metatrochophora* II (rough sketch) seen from the dorsal side (off Ven, $^{23}/_{10}$-1938). — *G*. *Nectochaeta* (off Frederikshavn, NW. Kattegat, $^{31}/_{7}$-1939) and *H*. *Nectochaeta*, front part of larva (off Ven, $^{12}/_{8}$-1940). See further the text pp. 70—71.

The young Trochophores (fig. 32 A-C), which are capable of devouring large specimens of *Coscinodiscus* or even Lamellibranch larvae, are 300 to 400 μ long, exotrochous, with two red eyes, a greenish-brown pigmentation on the front part and on the anal segment, and a deep verdigris to navy blue colour marking the limits of the intestine. The *Metatrochophora* I (fig. 32 D-F), 510—530 μ long, has a dark-brown pigmentation on the ventral side of the prostomium. A reddish-brown border of pigment separates the prostomium from the first body segment, and reddish-brown pigment covers the anal segment. Two dark-red eyes, a very large mouth, olive- to verdigris-coloured intestine, and — in the hindmost part of the intestine — a deep navy-blue colour. The *Nectochaeta*, finally (fig. 32 G-H, 33), 770 μ long, with 7 chaetigerous segments, has two reddish-black eyes, reddish-brown pigment on the hindmost corners of the prostomium and on the anal segment, olive-green to verdigris-coloured intestine of a deep navy-blue colour near the anus. The pharynx is distinctly seen. Both the prototroch and the teletroch persist, and seem to be rather active.

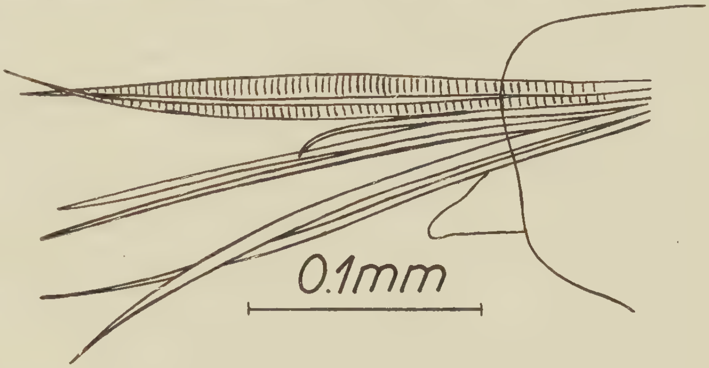


Fig. 33. *Nephthys ciliata* Müller. A single parapodium of the *Nectochaeta* larva shown in fig. 32 G.

Larvae of this species occur in our samples taken off Ven on: $^{10}/_{1}$-37 (3 spms.); $^{12}/_{3}$-38 (8 spms.); $^{23}/_{10}$-38 (1 spm.); $^{25}/_{3}$-39 (55 spms. in all stages of development); $^{10}/_{4}$-39 (1 spm.); $^{17}/_{5}$-39 (1 spm.), and $^{12}/_{8}$-40 (several specimens), and off Helsingør on: $^{2}/_{12}$-41 (3 Metatrochophores); $^{19}/_{12}$-41 (12 Trochophores and Metatrochophores); $^{3}/_{1}$-42 (335 young Trochophores); $^{31}/_{1}$-42 (250 mostly older larvae); $^{21}/_{2}$-42 (25, mostly older larvae); $^{21}/_{3}$-42 (3 young larvae); $^{10}/_{4}$-42 (3 spms.); $^{27}/_{4}$-42 (1 spm.), and $^{15}/_{5}$-42 (5 spms.). Thus the main season seems to be the winter and early spring, but larvae may also be found in the actual summer months and in the autumn. This is in good agreement with the vertical distribution of the adults, which thrive in the Baltic as well as in the Kattegat water.

Nephthys coeca Fabricius. Northern and middle parts of the Sound, occasional specimens.

Reproduction: A. Literature. McIntosh (1927, p. 76) states: "Ova well developed in the cælom of a female and 0.00021 in. in diameter, 15th November", and figures (fig. 22—23) the egg and early larva of *Nephthys coeca*. His figures, however, are too rough to allow of a closer identification. From plankton taken off Scheeveningen and den Helder in February to May Hofker (1920—22, p. CLVI) describes, without figures, larval Metatrochophores and Nectochaetes of *Nephthys* sp., which he supposes should be referred to *Nephthys coeca*. The *Metatrochophora* is rather large, without the green pigment found in the larva referred to *Nephthys hombergi* (which see), with a light-brown pigment, a high umbrella, and a blue colour in the hindmost part of the intestine. The *Nectochaeta* has nine chaetigerous segments (two types of setae), reddish-brown pigment, and a blue hindmost part of the intestine.

B. Own remarks. On $^{5}/_{8}$-39 five young and eight older larvae were taken in our plankton samples off Ven. The larvae (fig. 34 A-B), which differ from those referred here to *Nephthys ciliata*, have only been found in this single main series during our whole four-year investigation. As, however, the Trochophores among them seem to show that the larvae originate from the neighbourhood, and as *Nephthys coeca* is the only species of *Nephthys* which — apart from *Nephthys ciliata* was found in the adult stage as far southward as Ven, it seems most reasonable to refer the larvae to *Nephthys coeca*. However, no definite proof can be given. Only the *Nectochaeta* stage was sketched, but the younger larvae showed an unbroken chain of developmental stages which allowed the reference of all the larvae to the same species. The *Nectochaeta* (fig. 34 A-B) with seven chaetigerous segments differed from that referred to *Nephthys ciliata* by having olive-green pigment equally distributed over the front part of the prostomium and by having an olive-green anal segment. At the base of the prototroch there was a reddish-brown pigment band, and at the base of the teletroch a greenish-brown band. Faint brown pigment spots were seen at the boundaries between the segments on the ventral side. The pharynx was large, and the contents of the whole intestine were of a navy blue colour. Two black eyes. Prototroch and teletroch still persisted and seemed to be rather active. — The larvae referred by Hofker (l. c.) with some doubt to this species (see above), agree with the larvae from the Sound in the high umbrella and the blue colour of the hindmost part of the intestine, but while green pigment was absent in Hofker's larvae, green pigment together with brown and reddish-brown pigment were found in our larvae from the Sound. Hofker's description may as well refer to larvae of *Nephthys ciliata*, and it is therefore impossible to decide which species this author had before him.

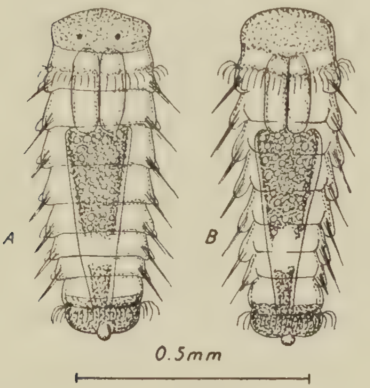


Fig. 34 A-B. *Nephthys coeca* Fabricius. Nectochaetes from plankton off Ven, depth 18 to 0 m, caught on $^5/_8$-1939 (drawn from life on $^6/_8$). — *A*. From the dorsal side. — *B*. From the ventral side.

Nephthys incisa Malmgren. Northern part of the Sound. (Kind information from Dr. Eliason, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

Nephthys longisetosa Ørsted. Northern part of the Sound, not common.

Reproduction: Unknown in the literature. No observations from the Sound.

Nephthys hombergi Aud. and Edw. Northern part of the Sound, not common.

Reproduction: A. Literature. Fuchs (1911) describes and figures the young larval stages of this species. Larvae were reared from artificially fertilised eggs and were kept in jars with filtered sea-water. It proved impossible to feed the larvae, which soon died. The eggs were opaque, somewhat flattened at the poles. Good figures of larvae two days old (Fuchs l. c., fig. 1), six days old (fig. 2), and fourteen days old (fig. 3). The larvae fourteen days old were still in the *Trochophora* stage and had brown and black bands of pigment. — Wilson (1936a, p. 305 –310) tried also artificial fertilisation (in June to September) and made the same experience as Fuchs, viz. that the larvae would not feed and grow beyond the *Trochophora* stage. The unsegmented egg was 112 μ across, and the larva began to swim 12—16 hours after fertilisation. Wilson's fig. 1 (l. c.) shows the larvae four days old. In 1940 Wilson again tried to rear the larvae of this species, but in vain (cf. Journ. Mar. Biol. Assoc., Vol. 24, p. 692). — From plankton taken off den Helder (Holland) in May Hofker (1920—22, p. CLVI) describes, without figures, *Nephthys* larvae, which he states should most likely be referred to *Nephthys hombergi*. Characteristic of the *Trochophora* is a green pigmentation arranged in three rings round the anus. The larvae with three segments have a prototroch as well as a paratroch (telotroch), and the *Metatrochophora* with seven segments has two black eyes, brown pigment round the base of the prototroch, a distinct neurotroch, and green anal pigment. The "*Nectotrochophora*" has a characteristic head flattened in front, green pigmentation on the anal segment, a terminal "bud" on the anal segment, and three types of setae in each parapodium.

B. Own remarks. Nothing is known about the reproduction of this species in the Sound, but as the youngest Trochophores of the Polychaeta in our samples were not examined individually, such Trochophores may have been overlooked. Dr. H. Blegvad has kindly informed me that females with large eggs occur in the western Limfjord from the end of May to the beginning of September, with an apparent maximum in July. In a female from the Sound he found large eggs on $^{2}/_{6}$-26. Thamdrup (1935) found specimens with eggs on $^{17}/_{3}$-34 at Skallingen (southwestern Jutland). Erik Smidt, studying the bottom animal larvae off Esbjerg, where *Nephthys hombergi* seems to be the only species of *Nephthys* found — or is at least absolutely dominant — on $^{21}/_{7}$-42 found several larval *Nephthys* in the plankton and has kindly placed his sketches at my disposal. The larva — a *Nectochaeta,* 510 μ long (fig. 35 A-B) with 6 chaetigerous segments — has two black eyes, and a very broad prostomium flattened in front and with light-brown pigment on the dorsal as well as the ventral side. Dark brown pigment on the dorsal side, and along the sides and the hindmost corners of the prostomium. A dark brown border on the ventral side marks the boundary between the prostomium and the first chaetigerous segment. The colour of the intestine has not been noted. The anal segment is provided with a very characteristic dark-brown pigmentation (cf. fig. 35 A) arranged round the anus. This pigmentation, observed in several larvae, seems to be the best character distinguishing this larva from those of *N. ciliata* and *N. coeca.* The prototroch and the teletroch were still present.

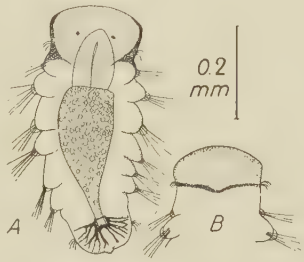


Fig. 35 A-B. *Nephthys hombergi* Aud. & Edw. Larva from plankton near Esbjerg, SW. Jutland, taken on $^{21}/_{7}$-1942 (sketches placed at my disposal by Mr. Erik Smidt).

The *Nectochaeta* described and figured here seems to agree fairly well with that referred to *N. hombergi* by Hofker (see above). They agree in their flattened front part of the head, in the brown pigment round the base of the prostomium, and in the heavy pigmentation round the anus. This pigment, however, seems to be brown in the Esbjerg larvae and green in the Dutch larvae, but this difference may probably be due to the larva having been seen in transmitted or in direct light respectively. After all it seems likely that Hofker (l. c.) is right in referring his larva to *N. hombergi.*

General Remarks on the Reproduction in *Eunicidae.*

Several observations of Eunicid larvae are available in the literature, and several facts are known concerning the egg-laying and the larvae. — 1) The eggs: In the genus *Eunice* the eggs are shed freely in the water during the swarming period of the adults. The conditions in the "Palolo", *Eunice viridis* (Woodworth 1907) are especially well known. Other examples are: *Eunice fucata* (Mayer 1908, 1912) and *E. harrassi* (Herpin 1924a, 1925). In *Diopatra neapolitana* (Syn. *D. cuprea*) Monro (1924, p. 194) found developing eggs and post-larval and young worms in the tubes of the mother animals. During his observations young worms were seen leaving the tube of the mother to form a tube of their own. Lo Bianco (1899, p. 485) in the same species found gelatinous, irregular, brown egg-masses, one centimeter across, each containing many small yellowish eggs, fixed to the mouth of the tubes of the mother animal in April to June. ANDREWS (1891) and TREADWELL (1921) describe the long cylindrical jelly masses in which the eggs are laid in *Onuphis magna*, and state that the hatching larvae (figured) swim freely in the water. CLAPARÈDE and METSCHNIKOFF (1869, p. 20) describe "die eingefangenen Eier" of an Eunicid, which they refer either to the genus *Lumbriconereis* or to the genus *Notocirrus*, and their description seems to show that the eggs in question occur singly in the plankton. FEWKES (1883, p. 197) has found gelatinous egg clusters belonging to the genus *Lumbriconereis*; his investigations will be summarised below. — 2) The larvae: In accordance with its spawning habits the genus *Eunice* has a pelagic larval stage, which, however, is rather short. In *Eunice harrassi* (HERPIN 1924 a, 1925) this pelagic stage will only last for one week, and the pelagic larvae will feed on their own contents of yolk — not on plankton. In the other genera of Eunicids the tendency to a reduced pelagic stage (or to a total non-pelagic development) seems to be still more pronounced. All the larvae of *Ophryotrocha puerilis* (CLAPARÈDE and METSCHNIKOFF 1869, p. 22) were swimming near the bottom of the glass dishes and seemed to have no really pelagic stage. The larvae, which were referred by the same authors either to *Lumbriconereis* or to *Notocirrus*, had lost all their cilia in the stage with only two chaetigerous segments. The larvae of *Diopatra neapolitana* (MONRO l. c.) are non-pelagic, and the same seems to be the case with the larvae of *Staurocephalus chiaji* (CLAPARÈDE and METSCHNIKOFF 1869, p. 24); larvae of this species, 800 μ long, had lost all their larval characters and all their cilia, and the whole jaw-apparatus as in the adults had developed. The larvae, which were referred by HÄCKER (1897) to the Eunicids, seem to belong to quite different families; the larva sketched in figure 4 by HÄCKER is probably a Polynoid larva.

The early development of the large jaw-apparatus characteristic of the adult Eunicids is a typical feature in all larvae within this group and distinct jaws will probably always be met with in the older pelagic stages.

Eunice (Leodice) pennata (O. F. MÜLLER) (= **E. pennata** EHLERS). Taken once off Ven. Reproduction: Unknown in the literature. No observations from the Sound.

Lumbriconereis fragilis MÜLLER. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Nothing is known about the reproduction of *L. fragilis*. LO BIANCO (1899), however, succeeded in making an artificial fertilisation of eggs of *Lumbriconereis impatiens* at Naples in May, and FEWKES (1883, p. 197) has given excellent figures and descriptions of the development of *Lumbriconereis* sp. from Newport. His observations may be summarised as follows: Gelatinous clusters glued together in spherical masses of slime and attached to the surface of the mud were found in June, July, and August, and proved to be the egg masses of *Lumbriconereis* sp. The embryos, which are of a greenish colour, develop inside the mass of slime to larvae "possessing spines which can be projected from the body, and a ring of cilia about the head", but they "have very limited movements, even when artificially set free from the cluster in which they are bound together". The figures given by FEWKES (l. c.) as well as his statement, that the development is quite similar to that of "*Arenicola marina*" described by SCHULTZE (1856) (= *Scoloplos armiger*), shows that the development is non-pelagic.

B. Own remarks. In spite of the very common occurrence of the adult *Lumbriconereis fragilis* in the Sound, not a single larval Eunicid was observed in our four years' samples. Accordingly there is hardly any doubt that the larval development is non-pelagic, as was also the case with the species mentioned above.

Glycera alba Rathke. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Nothing is reported in the literature about the reproduction of *Glycera alba*; the only description of young larvae of Glycerids seems to be that of Fuchs (1911, p. 164—70) of the early larvae of *Glycera convoluta*. According to Journ. Mar. Biol. Assoc., 1940, vol. 24, p. 692 Wilson is going to publish a paper on the larvae of *G. convoluta*. Fuchs (l. c.) mentions that "the egg of *Glycera* is discoidal, and it does not swell up in sea water. It is granular, but comparatively transparent, with a lighter coloured nucleus". The fertilisation was artificial, and the method used is described. "Swimming blastulae of *Glycera convoluta* appear some ten hours after fertilization, and the trochal ring is formed in twenty-four hours". A description and excellent figures of young larvae up to the late *Trochophora* stage (10 days old) with its green-pigmented dots are given. The Metatrochophores and the Nectochaetes of this species have never been described. Aiyar (1933, p. 115) describes and figures Trochophores of *Glycera* sp. from the Madras harbour (India). They are able to devour large specimens of *Coscinodiscus*, just as is stated for larvae of *Nephthys ciliata* from the Sound (see this paper pp. 70—71). The same author (l. c., p. 115) describes and figures a full-grown larval Glycerid, which he refers to "*Eone* sp." (Locality: Madras harbour), the transversely gathered prostomium and the four terminal antennae of which closely resemble the larval type occurring in the Sound and here referred to the genus *Glycera*.

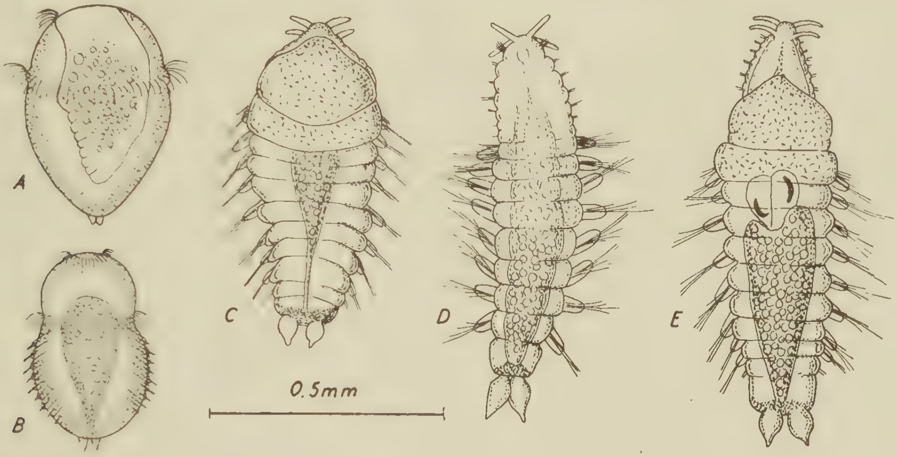


Fig. 36 A-E. *Glycera alba* Rathke. Larvae from plankton, drawn from life on the day of capture. — *A. Trochophora*, off Ven, depth 18 to 0 m, taken on $^{8}/_{10}$-1938 (rough sketch, the scale of magnification not quite reliable). — *B. Metatrochophora* II. From the Copenhagen harbour, $^{22}/_{11}$-1938 (rough sketch by Mr. Erik Smidt). — *C* to *E. Nectochaeta* larvae, taken off Ven, on $^{18}/_{12}$-1938, C and E from the dorsal side, D from the ventral side.

B. Own remarks. In our four years' series several larvae are present, from young Trochophores to late Nectochaetes (fig. 36 A-E), which could be referred without difficulty to the *Glyceridae*. The Nectochaetes, which had 8—9 chaetigerous segments, showed already the typical features of the adult *Glyceridae*. The conical segmented prostomium with four terminal tentacles was distinctly seen, and each of the segments of the prostomium was provided with bristles. Such bristles are also seen in Aiyar's *Eone* larva from Madras and in Ehler's (1864—68, pl. 24, fig. 2) drawing of the prostomium of the adult *Glycera tesselata*, and they must be supposed to be characteristic of the whole genus. The young Trochophores (fig. 36 A) are about 440—450 μ long; they have a band of apical cilia and a large prototroch. They are rather similar to the Trochophores of *Glycera convoluta* (Fuchs 1911, fig. 8–9), but the anal cirri are already visible. The pigmentation is reddish-brown, not green as in *G. convoluta*, and the shape is somewhat more slender than in this species. The *Metatrochophora* II, 400 μ (fig. 36 B) to 500–550 μ long, with six to nine chaetigerous segments is like the *Trochophora* in all other respects. The *Nectochaeta* stage, 840 μ long (fig. 36 C-E), is very characteristic. The parapodia on the 8–9 segments are well developed. The prostomium has seven bundles of bristles on each side, and the four slender tentacles are placed as terminally as possible. The first chaetigerous segment and the segment in front of it form a shield-like swelling on the dorsal side, which in contracted larvae (fig. 36 C) may cover the prostomium. In one of the larvae (fig. 36 E) the pharynx was very distinct, and the first traces of the jaws were seen. The intestine was reddish-grey, the larva as a whole was yellowish-white to pink, while the "shield", the hindmost part of the anal segment, and the middle part of the ventral surface had reddish-brown pigmentations. Round the parapodia were yellowish-brown spots of pigment. Two lancet-shaped anal cirri. No eyes.

Among the adult species of *Glyceridae, Glycera alba* and *Goniada maculata* are very common throughout the Sound, while the third species, *Glycera lapidum*, is rather rare. *G. alba* seems to be somewhat commoner than *Goniada maculata*, the latter being very rare in the southern part of the Sound. Further, *Glycera alba* is much more common in the Baltic water than *Goniada*. This is of importance if we are to identify the larvae. For these larvae were observed on three occasions (November 1938, January 1939, and January 1940) in the harbour of Copenhagen, where Baltic water predominates, and this circumstance in connection with McIntosh's statement (1910, monogr., p. 466), that *Goniada maculata* has "large ova", and the fact that a pelagic development was known beforehand within the genus *Glycera*, seems to confirm the assumption that the larvae from the Sound belong to *Glycera alba*. However, nothing definite can be stated.

Such larvae were present in our four years' samples taken off Ven on the following dates: $^{6}/_{12}$-36 (3 spms.); $^{19}/_{12}$-36 (1 spm.); $^{14}/_{11}$-37 (4 spms.); $^{18}/_{12}$-37 (7 spms.); $^{6}/_{1}$-38 (4 spms.); $^{8}/_{10}$-38 (4 spms.); $^{4}/_{12}$-38 (3 spms.), and $^{16}/_{9}$-39 (3 spms.), and off Helsingor on: $^{19}/_{12}$-41 (3 Nectochaetes); $^{31}/_{1}$-42 (15 spms. in all stages of development), and $^{21}/_{2}$-42 (7 mostly older spms.). The main season for larval occurrence is accordingly November to February (also in the harbour of Copenhagen); not a single larva is present from the months February to September. All stages of development seem to be equally frequent in the plankton, and the larvae seem never to occur in large numbers. The occurrence in the winter should probably be viewed in connection with Aiyar's (1933, p. 115) observation that *Glycera* larvae may feed on *Coscinodiscus* (cf. *Nephthys ciliata*). – A ripe male of *Glycera alba*, taken off Hellebæk, 35 m depth, on $^{12}/_{9}$-41, spawned large clouds of ripe sperms when placed in formalin.

Glycera lapidum de Quatrefages. Northern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. McIntosh (1910, monogr., p. 480) states that "specimens procured in Bressay Sound in July were laden with nearly ripe ova".

B. Own remarks. Nothing is known about the reproduction in the Sound.

Glycera goesi Malmgren. Northern part of the Sound. (Kind information from Dr. Eliason, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

Goniada maculata Ørsted. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. McIntosh (1910, monogr., p. 466) found "large ova in July off the SW. of Ireland".

B. Own remarks. The frequency of this species in the adult stage in the Sound suggests that the larvae, if pelagic, would occur in several specimens in our samples. As mentioned above only one species of Glycerid larvae was taken in our plankton; I have referred this larva to *Glycera alba* (which see) which is still commoner in the adult stage than *Goniada maculata*. If I am right in this identification, it means that *Goniada maculata* reproduces by non-pelagic larvae in the Sound. This assumption seems to be supported by McIntosh's statement (l. c.) concerning the "large ova" of this species.

Aricia cuvieri Aud. and Edw. Two finds in the northern part of the Sound.

Reproduction: A. Literature. Nothing is known about the reproduction of this species.—The closely related species *Aricia foetida*, however, has been studied rather thoroughly and the results have been published by Lo Bianco (1899), Salensky (1883), Schaxel (1912), and Eisig (1914). Below a brief summary of these papers will be given; all the observations are from Naples. Spawning season January to June, with a maximum in March. The sexual products in ripe specimens are seen through the body wall; sperms white, eggs reddish-brown to yellowish-green. A female which has spawned will spawn again four weeks later, and the male will fertilise the eggs at the very moment at which they are spawned. The egg mass is gelatinous, cylindrical, six to eight cm long (shaped like the egg mass of *Loligo*), and fixed to the sand where the adults live. Each egg mass contains numerous eggs, which are at first greenish, later on yellowish; the egg masses develop readily in glass dishes. The interval from the fertilisation to the hatching of the larvae varies according to the temperature from six days (Salensky l. c.) to 6—12 days (Schaxel l. c.) or two to three weeks (Eisig l. c.). Salensky states that the hatching larvae live on their own contents of yolk during the first six weeks; he figures a hatching vermiform larva with slight traces of a prototroch, which seems to prove that the development is non-pelagic or at least reduced. Schaxel mentions the "hatching vermiform Trochophores", and Eisig mentions the "swimming heliotropic larvae", which, when about 14 days old, will seek to the bottom. As the space of time given by Eisig for the larval development within the egg mass by far exceeds that given by the other authors, it seems probable that Eisig operated with especially low temperatures, and that he has estimated the duration of the swimming stage, fourteen days, too high. Schaxel states that one and a half weeks after hatching the larvae take nourishment from the mud of the bottom. All this seems to show that the larva has a short swimming stage, that it is probably not really pelagic but swims about near the bottom all the time, taking no food from the plankton. Similar larvae of *Scoloplos armiger* are much more ciliated, but are nevertheless known to develop without any pelagic stage.

B. Own remarks. *Aricia cuvieri* is very rare in the Sound. Besides the single adult specimen taken between Kullen and Gilleleje in 1916 Eliason (1920, p. 38), two adult specimens were secured during our investigations off Hellebæk in the summer of 1941. Nothing is known about the reproduction in the Sound, but from the East Greenland fjords, where this species is a type-animal (4—12 spms. per sq.m from a depth of 3—45 m, cf. Thorson 1936, p. 28) and whence regular plankton series are at hand from the whole year, not a single larva was found in the plankton which could be referred to this genus. Such vertical planktonic series taken during a whole year in East Greenland are at hand from the inner fjords as well as the outer coast; it can be taken for granted that this species has a non-pelagic development there, which is in good agreement with the much reduced larval life of *Aricia foetida* and the non-pelagic development of the related species *Scoloplos armiger*.

Scoloplos armiger Müller. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Max Schultze (1856) has described and figured the egg masses of this species and referred them to *Arenicola marina*. Cunningham and Ramage (1888, good figures), Mau (1882), Hornell (1891), Ehlers (1892), McIntosh (1890), Leschke (1903), Delsman (1916), Eisig (1914), Grooth (1907, good figures), Thamdrup (1935), and Linke (1939, good figures) have studied the reproduction and development of this species; their results can be summarised as follows: Spawning season near Holland from the end of February to the middle of April, near Scotland in February, in the Bay of Kiel in May to June, at Jadebusen from the end of March to the middle of May, and at Skallingen from March to May. The eggs are laid in gelatinous, pear-shaped cocoons. Each cocoon is 2 cm long and 1 cm broad, and is attached to the sand by a tough string about 5 cm long (beautiful figures in Linke 1939, p. 249). A female is able to spawn more than one cocoon. The individual egg mass contains 400—1000 greenish to reddish-brown eggs, and as a ripe female contains 3.000—5.000 eggs, each female must be supposed to spawn several cocoons. The larvae will remain in the cocoon until three weeks after fertilisation, and will then hatch in the crawling stage without any pelagic life, though short cilia and ciliary bands are still present. When hatching, the larvae are more than 600 μ long; the bristles will not appear until the larva is in the crawling stage. — Hofker (1920—22, p. CLXII) refers free-swimming larvae up to 400 μ, taken in May off den Helder (Holland), to this species, as they agree with the description and figures of Grooth (l. c.).

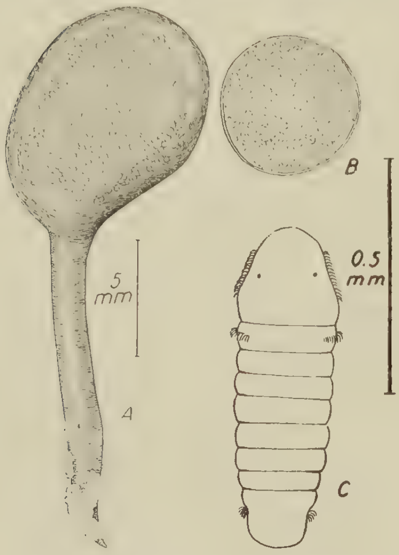


Fig. 37 A-C. *Scoloplos armiger* Müller. —*A*. Egg mass with detritus adhering to its stalk. Taken off Hellebæk, on hard sand bottom, at a depth of 10 m, on $^{10}/_{4}$-1942 (drawn from life on $^{12}/_{4}$-1942). The egg mass contained about 1250 eggs. — *B*. Uncleaved egg from the egg mass fig. 37 A. — *C*. Old embryo from an egg mass taken off Hellebæk, sand bottom, depth 10 m, on $^{27}/_{4}$-1942 (drawn from life on $^{28}/_{4}$-1942). See the text pp. 78—79.

B. Own remarks. In two dredge hauls taken off Hellebæk, at 9—10 m, hard sandy bottom, on $^{10}/_{4}$-42, 8 egg masses of this species were secured. Two of these were undamaged (fig. 37 A), and on examination proved to agree in all details with those described by the authors cited above. They had the shape of a stalked balloon (fig. 37 A). In the two undamaged egg masses the balloon, which had a diameter of about 1 cm, contained about 1250 and 800 eggs respectively. The slimy stalks, nearly 2 mm across, were about 15 mm long. The pinkish-yellow eggs (fig. 37 B) were 300 μ across, quite opaque and had a very thin egg membrane. The egg masses found were in the first stages of development, and the spawning had probably not commenced until late in March or early in April. On $^{27}/_{4}$-42 three more egg masses were secured from the same depth and the same locality. One of them contained young larvae, the other two older larvae apparently almost ready to hatch. These larvae (fig. 37 C), 650 μ long, were yellowish-white, solid, with two small red eyes. The first eight body segments had commenced to form, but still no bristles had appeared. On the prostomium was a broad transverse band of short cilia, and such short cilia were also present on the first body segment, on the anal segment, and in a longitudinal band along the ventral side. The other cilia, seen for instance in the figures of GROOTH (l. c.), were not observed in our larvae; they may probably appear later together with the bristles. The mouth had not yet formed, and accordingly the young take no food from outside. In the large number of dredge hauls taken in June-July-August for a great number of years such egg masses were never found. Hence the spawning must be limited to the early part of the spring. — In Sallingsund (the Limfjord) a spawn containing large young specimens was taken on $^{21}/_{5}$-24 (according to kind information from Dr. H. BLEGVAD).

Nerine foliosa (AUD. and EDW.). One specimen found at Hellebæk earlier than 1893. The species is also known from the Swedish west coast. — During the summer of 1941 several of the species recorded in the literature prior to 1890 were found at Hellebæk, and several forms only known in a few specimens in the early literature proved to be rather common in the same localities at the present day. So far we have not found *Nerine foliosa*, but since only some few samples from Hellebæk are at hand, this species may occur in a much larger number than it would appear from the one specimen recorded in the literature.

Reproduction: A. Literature. CUNNINGHAM and RAMAGE (1888, p. 636—37, pl. 36, fig. 1 D and E) figure a ripe, unfertilised egg and an egg in the four-cell stage (under the synonym of *Nerine coniocephala*), and mention that the vacuoles are at first found inside the yolk mass, but as soon as the egg is spawned, the yolk-mass will concentrate in the middle of the egg, and the vacuoles will fill up the space between the yolk-mass and the fenestrate egg membrane, thus making the egg able to float in the water. No size of the eggs is given, nor is the magnification stated in the text to the figures. AGASSIZ (1867, p. 318 to 343, fig. 39—42) describes and figures planktonic *Nerine* larvae, saying that "the species of *Nerine* here investigated is probably the *Nerine coniocephala* of JOHNSTON" (= *N. foliosa* (AUD. and EDW.)). — Much better known are the egg and the larva of *Nerine cirratulus* (cf. CUNNINGHAM and RAMAGE (1888, fig.), CLAPARÈDE and METSCHNIKOFF (1869, fig.), MESNIL (1916), LO BIANCO (1899, p. 488), and HOFKER (1920-22, p. CLX)), and as the data given for this species may help to clear up some points as regards *Nerine foliosa* also, a brief summary will be given here. — *Nerine cirratulus* (DELLE CHIAJE) (Syn.: *Scolecolepis squamata* (ABILDGAARD)): the pelagic eggs laid singly have a well developed vitelline membrane covered externally with a reticulation of hexagonal meshes. The vitelline membrane persists at this stage and for some time afterwards, forming a cuticle for the larva and retaining its characteristic honeycomb-like reticulation of projecting ridges. The bands of cilia project through the vitelline membrane, and so does a tuft of sensory hairs in front of the prostomium. The larva is teletrochous with two red eyes and provisional larval bristles. The older larvae in the plankton are of a verdigris colour. CLAPARÈDE and METSCHNIKOFF (l. c., fig. 4 A) figure a planktonic larva with 37 chaetigerous segments, while the oldest larva figured by CUNNINGHAM and RAMAGE (l. c., fig. 2 I and J) has only twelve chaetigerous segments. The largest diameter of the egg with the young *Trochophora* inside is 310 μ (according to McINTOSH 1915, monogr.. pl. 94, fig. 5 and 6).

B. Own remarks. Eggs of the type described above are met with in fairly considerable numbers in the plankton in the Sound in January to April. The "eggs" found (fig. 38 A-G) included all stages from the nearly unsegmented stage to the late *Trochophora* with the first larval bristles. The vitelline membrane is bluish-grey, the yolk or the *Trochophora* inside is greenish-brown, the latter with a pair of dark reddish eyes. The largest egg-diameter varies from 310 to 350 μ, the largest breadth is about 260 μ, the smallest breadth about 190 μ, the egg membrane being somewhat compressed. Eggs in which the vitelline membrane has lost its original shape and has commenced to adhere to the *Trochophora* (fig. 38 G) were also found. Eggs in different stages of development are present in our four-year series taken off Ven on the following dates: $^{6}/_{1}$-38 (45 young eggs); $^{23}/_{1}$-38 (four eggs with large Trochophores and soft vitelline membrane); $^{3}/_{4}$-38 (five eggs); $^{18}/_{4}$-38 (9 eggs), and $^{19}/_{2}$-39 (20 eggs), and off Helsingor on: $^{19}/_{12}$-41 (7 Trochophores); $^{3}/_{1}$-42 (20 Metatrochophores); $^{31}/_{1}$-42 (4 Trochophores); $^{21}/_{2}$-42 (1 Trochophore); $^{10}/_{1}$-42 (6 Trochophores); $^{27}/_{4}$-42 (17 Trochophores); $^{15}/_{5}$-42 (1 Trochophore), and $^{4}/_{6}$-42 (3 Trochophores). Eggs of precisely the same appearance were observed in the harbour of Copenhagen in January 1940 (Erik Smidt 1944, p. 259), and Leschke (1903 p. 123, pl. 6, fig. 10) describes and figures, from the Bay of Kiel, an egg with a large *Trochophora*, which to all appearance seems to belong to the same species. Only two eggs were seen by Leschke, both on January 10th, 1901. All these dates seem to show that the species is decidedly a winter spawner with its main season from January to April. Eggs of the type mentioned here are known not only from *Nerine foliosa* and *Nerine cirratulus*, but also from *Scolecolepis fuliginosa*. (In the summer of 1941 this species was found in the Isefjord by Erik Rasmussen. Thus it is known from Danish waters, though it is still unknown from the Sound). The eggs of the latter species, however, are much smaller — largest diameter 120 to 160 μ — than those found in the Sound, while our eggs from the Sound agree well in size with those of *Nerine cirratulus* (310 μ). As, however, *Nerine foliosa* is the only species of *Nerine* known from the Sound, it seems most reasonable to refer the eggs to this species, the egg size of which is not given in the literature.

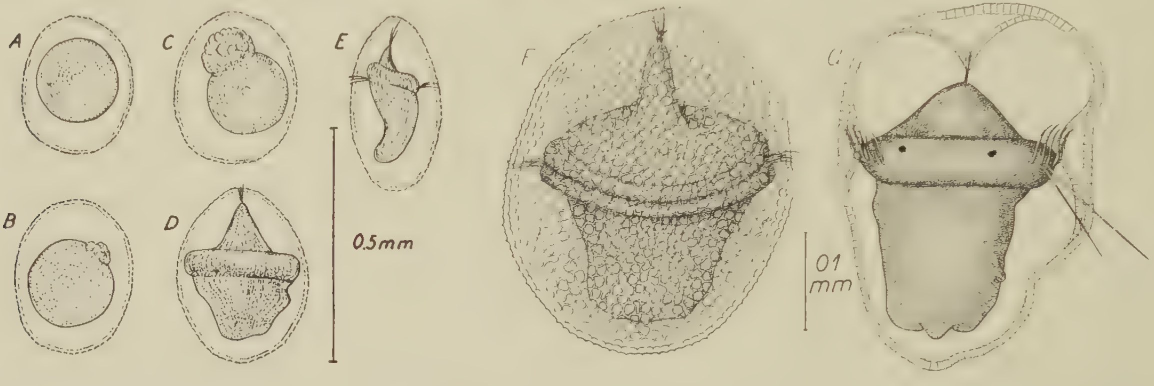


Fig. 38 A-G. *Nerine foliosa* (Aud. & Edw.). Eggs and young embryos from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{6}/_{1}$-1938. — *A*. Undeveloped egg, *B* and *C* eggs in different stages of cleavage. — *D*. *Trochophora* inside the egg membrane in front view. — *E*. A similar stage seen in lateral view. — *F*. More detailed sketch of a *Trochophora* inside the reticulated egg membrane, seen in front view. — *G*. Transitional stage between *Trochophora* and *Metatrochophora* I. The egg membrane has commenced to adhere to the animal (optical section).

From $^{19}/_{2}$-39 ten large larvae, and from $^{4}/_{3}$-39 fifty large larvae are present in our samples (fig. 39 A) from Ven, which seem to agree fairly well with the figures given by Agassiz (1867, fig. 39—41); the larva was identified by him as belonging to *Nerine foliosa*. Here, also, the larvae of *Scolecolepis fuliginosa* can be disregarded, as this species will metamorphose with 14 chaetigerous segments (see below), while our large larvae in the plankton have normally at least 18 segments. When metamorphosing, *S. fuliginosa* has commenced to develop frontal horns on the prostomium, while the prostomium of our larva with 18 segments is rounded. However, the pelagic *Nerine* larvae figured have a much larger number of chaetigerous segments than larvae of *S. fuliginosa*, viz. up to 37 segments in *N. cirratulus* and up to 19 segments in *N. foliosa*, the latter number agreeing closely with our larva (fig. 39 A) from the Sound. The number of chaetigerous segments, the resemblance to Agassiz's figures (l. c. fig. 40—41), and the fact that the larval season is a direct continuation of the season of occurrence for eggs and *Trochophora* larvae referred to *Nerine foliosa*, seem to indicate that the larvae should be referred to this species also.

This large larva (fig. 39 A) is rather broad in front. The eyes (three pairs) are black, the two lateral pairs nearly fused. The prostomium is of a faint yellowish-brown colour, the pharynx has a longitudinal line of reddish-brown pigment, the intestine is yellowish-green, the "rectum" is black, and transverse lines of greyish-brown pigment are found on the hindmost 12 or 13 segments. Eighteen pairs of chaetigerous segments with long, coarse larval bristles are present.

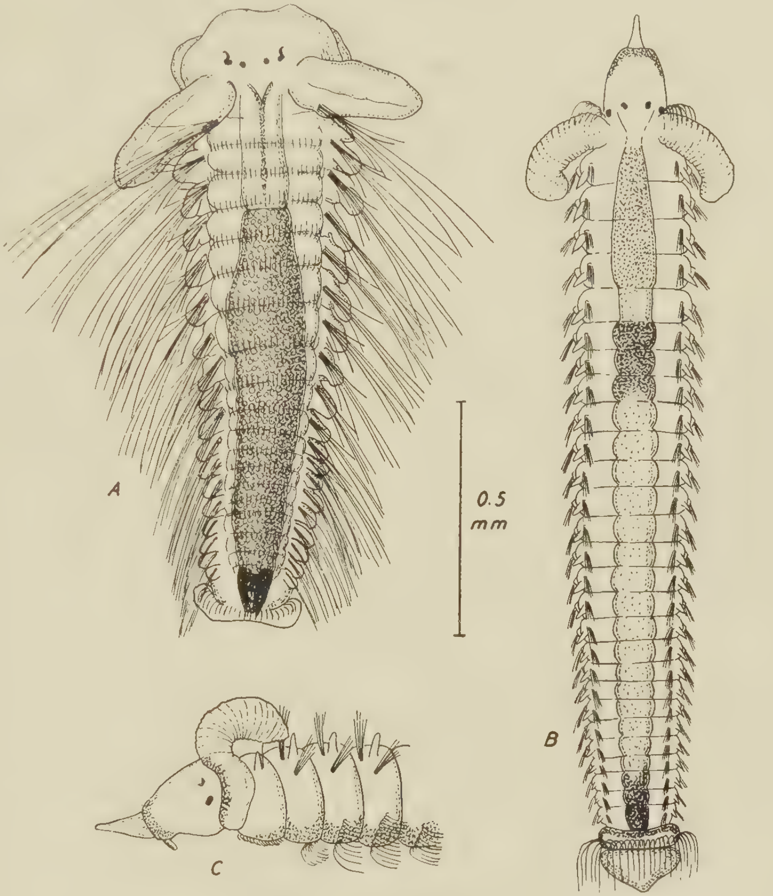


Fig. 39 A-C. *Nerine foliosa* (Aud. & Edw.). Larvae from plankton, drawn from life. — *A*. *Nectochaeta* of medium size, seen from the dorsal side (probably somewhat squeezed by the cover glass); off Ven, depth 18 to 0 m, caught and drawn on $^{4}/_{3}$-1939. — *B* and *C*. Larva in the oldest planktonic stage known, seen from the dorsal side (B) and from the left side (C, front part of the body only). Taken between Hellebæk and Kulla Gunnarstorp, depth 30 to 0 m, on $^{2}/_{12}$-1941 (drawn on $^{3}/_{12}$-1941).

On $^{2}/_{12}$-41 a single specimen of a large Spionid larva was found in plankton taken between Hellebæk and Kulla Gunnarstorp, at 30—0 m. In shape as well as in structure (but not in pigmentation) this larva (fig. 39 B-C) bore a very close resemblance to that described by Claparède and Metschnikoff (1869, p. 11, pl. XII, fig. 4 A) as belonging to *Nerine cirratulus*. Our larva had 27 chaetigerous segments and in direct light showed yellow pigment on the front part of the head, and yellow and green pigment on the anal segment. The eyes were reddish-black. In the first four body segments the intestine was of a green colour, followed by a yellow colour in the fifth segment, and by a black colour in segments 6—8, then came a colourless part in segments 9—24, while the hindmost three segments showed a deep black colour. As the large larva of *Nerine cirratulus* figured by Claparède and Metschnikoff (l. c.) differs in colour (verdigris) and in larval bristles from our large larva from the Sound, and as this species is also unknown from the Sound, it seems natural to regard the larval stage in question as the oldest planktonic stage of *Nerine foliosa*. Agassiz's figure (1867, fig. 42) seems to support this supposition. The larva of Agassiz has 36 chaetigerous segments, four eyes, and an acute prostomium. All these characters agree well with our larva from the Sound, and the larvae described by Agassiz are also referred to *Nerine foliosa*. It is, however, surprising that the only larva nearly ready to metamorphose was taken early in December, while the spawning of the adult species in the Sound seems to take place within the period from the end of December to April. Probably this large larva had been carried to the Sound from breeding places in northern Kattegat, while most other larvae of this species secured from the Sound are derived from parents inhabiting the Sound itself or its nearest neighbourhood.

Scolecolepis ciliata (Keferstein). Two adult specimens were found off the point of Kronborg, Helsingør, depth 25 m, on $^1/_7$-41.

Reproduction: A. Literature. Nothing is known about the reproduction of this species. — In other species of the genus, however, the reproduction has been well investigated, thus for instance in *Scolecolepis fuliginosa* (Claparède). As this species was found by stud. mag. Erik Rasmussen in the Isefjord in the summer of 1941 and hence may probably also be found in the Sound, a brief summary of its mode of reproduction will be given here on the basis of papers by Lo Bianco (1909), Claparède and Metschnikoff (1869, with figures), McIntosh (1915, monogr.), Day (1934, with figures), and Day and Wilson (1934): *Scolecolepis fuliginosa* spawns its eggs in a small gelatinous nest of irregular shape floating at the surface of the water. Often a large number of ripe animals will crowd together and spawn sperms and eggs in a common mass of slime. Spawning season at Naples from October to April. Larvae from eggs spawned in captivity may feed and grow on *Nitzschia*. The shape of the egg is variable, normally the egg is 120—160 μ long and 100 μ broad; the vitelline membrane has a reticulation quite similar to that described above for *Nerine cirratulus* and *N. foliosa*, and as in these species, the cilia and — in the *Metatrochophora* — the larval bristles will project through the vitelline membrane, which will later on form the cuticle of the larva. Less than 24 hours after fertilisation swimming Trochophores are about 200 μ long, their colour is brown. Larvae 48 hours old already have two chaetigerous segments; larvae four and a half days old have three segments; Larvae nine days old have four setigers and are about 400 μ long. Eight-setiger larvae (20 days old) about 770 μ long, 10-setiger larvae (24 days old) about 870 μ long, and 14-setiger larvae (34 days old) 1060 μ long are also pelagic, but the 14-setiger stage will normally metamorphose and sink to the bottom. Excellent figures of all these stages are given by Day (l. c.). Further Day and Wilson (l. c.) have shown that larvae in the 14-setiger stage will make their way to the bottom and begin to metamorphose as soon as a suitable type of bottom is found. When such a bottom is lacking, however, the larvae will continue their planktonic life for a week or two, until a suitable substratum is found. Day (1937) states that young of this species may, "after an abnormally prolonged larval period, actually metamorphose and grow while swimming in a plunger-jar", thus having a chance to spread also after metamorphosis. — On another species, *Scolecolepis vulgaris* Johnston, McIntosh (1915, monogr,. p. 160) has made the following observations: "On May 10th a female was laden with ova having the peculiar spini-reticulate capsule (pl. 94, fig. 13), and some were not quite round".

B. Own remarks. As mentioned above, the method of reproduction in *Scolecolepis ciliata* is entirely unknown, but the related species hitherto investigated seem to show that pelagic ova with a reticulated egg-membrane are typical of the whole genus, as they are of the genus *Nerine*. In our four years' samples, however, no eggs are present which can be referred to this species (see the remarks under *Nerine foliosa*), and the single find from Helsingor seems to suggest that even the adult animal is rather rare in the Sound.

Pygospio elegans Claparède. Very common, especially on sandy bottom in shallow water in the northern and middle parts of the Sound.

Reproduction: A. Literature. Eliason (1920) records *Pygospio seticornis,* not *P. elegans,* from the Sound, but Söderström (1920) has shown that *Pygospio seticornis* comprises the males and *P. elegans* the females of one and the same species, which should be termed *Pygospio elegans* Clap. Allen (1915) reports breeding in March at Plymouth. Söderström gives the following data regarding the egg capsules and the development of this species near Bohuslän: the eggs are laid in a long row of small capsules which are in contact with each other. These capsules numbering up to 16 — the same number as the number of egg-bearing segments in the mother animal — are found in the tube of the mother animal, where each capsule is anchored by a thin thread and contains about 50—60 eggs 100 μ in diameter. Only 7 to 9 of these eggs develop into embryos, while the rest of them break up into pieces of yolk, which serve as nourishment for the developing embryos ("nurse-eggs"). The embryos develop into hunch-backed embryos, 200 μ long, 200 μ broad, and 200 μ high (Söderström, l. c., p. 188, fig. 117), with two pairs of parapodia, two pairs of eyes, a faintly developed prototroch, and a large content of yellow yolk in the stomach. The embryos rotate in the capsules, but are unable to perform large movements. These young embryos will develop inside the capsule until reaching a length of 1—1.2 mm and developing twelve chaetigerous segments, two pairs of eyes, and one pair of very short tentacles. Söderström is of opinion that the embryos may be still older before they leave the capsule than stated here, and he mentions the find of 20 small specimens with 16 chaetigerous segments crawling in a tube of *Pygospio.* The oldest stages found in the capsules are without the provisional larval bristles normally found in all pelagic Spionid larvae. Söderström (l. c. p. 191—193) discusses the paper of Mesnil and Caullery (1917), in which it is shown that *Spio filicornis* (see this species) has one type of egg capsules with pelagic larvae in the spring and one type in the late summer, which closely resemble those described by Söderström for *Pygospio elegans.* Leschke (1903, p. 122) has described and figured pelagic larvae of *P. elegans* from Kiel occurring in the plankton from November to April, and Söderström is of opinion that this supports the assumption that *Pygospio elegans,* like *Spio filicornis,* has both a pelagic and a non-pelagic type of larval development adapted to the different seasons of the year. No definite proof of this supposition is given, nor is it stated with certainty that Leschke is right in his above-mentioned identification. Linke (1939, p. 269) states that Spionid larvae (most probably belonging to *Pygospio elegans,* the only Spionid common in the area investigated) are frequent in the plankton in May by Jadebusen, where also young bottom stages of *Pygospio,* 3—5 mm long, are common in April to May. These facts seem to support Söderström's supposition of a pelagic reproduction in the spring.

B. Own remarks. The species is very common in the Sound on shallow sandy areas. In one of a series of tubes taken off Aalsgaarde at a depth of 2 m on $^{27}/_{6}$-41 were four undamaged egg capsules each with three to five very large, hunch-backed embryos of exactly the same size as figured by Söderström (l. c., p. 188, fig. 117), only that my larvae had six eyes (those of Söderström four eyes). All nurse eggs in the capsules had already been devoured. These observations show that the method of development described by Söderström for this species from Kristineberg is also exhibited by the species in the Sound. In materials from Aalsgaarde, taken on $^{27}/_{6}$-41, and from the Hittarp reef, taken on $^{27}/_{7}$-41, at a depth of 20 m, a few quite colourless Spionid larvae were observed partly swimming, partly crawling in and among the tubes of the adults. I had no chance to sketch them, but they were colourless and had 16 to 20 chaetigerous segments without long larval bristles. Larvae which agree in appearance with those met with among the parent tubes, are, however, very frequent in the Sound plankton whence sketches are at hand (fig. 41 E). Ten egg strings (fig. 40 A) from tubes taken off Julebæk, depth $^{1}/_{2}$ m, examined living on $^{16}/_{7}$-1945, contained in each capsule one to three embryos feeding on nurse eggs. The youngest of them where in the hunch-backed stage (three chaetigerous segments, three pairs of eyes, terminal ciliary ring) and were totally distended by pieces of yolk (fig. 40 B). These facts and the nearly total absence of small, pelagic *Pygospio*-larvae (type A, see below) during the actual summer time seem to support Söderströms' conjecture, that the species will reproduce in two different ways according to the seasons of the year. The oldest embryos from the Julebæk capsules (fig. 40 C) are about 700 μ long, with 8 to 10 segments with medium-sized bristles. They have ciliary tufts on the head, a ciliary ring on the anal segment and three pairs of eyes. Probably they where not yet ready to hatch, although they were able to swim, when dissected out. Normally they will no doubt hatch in the stage mentioned below as larvae of type B, i. e. as large larvae with a shortened pelagic life.

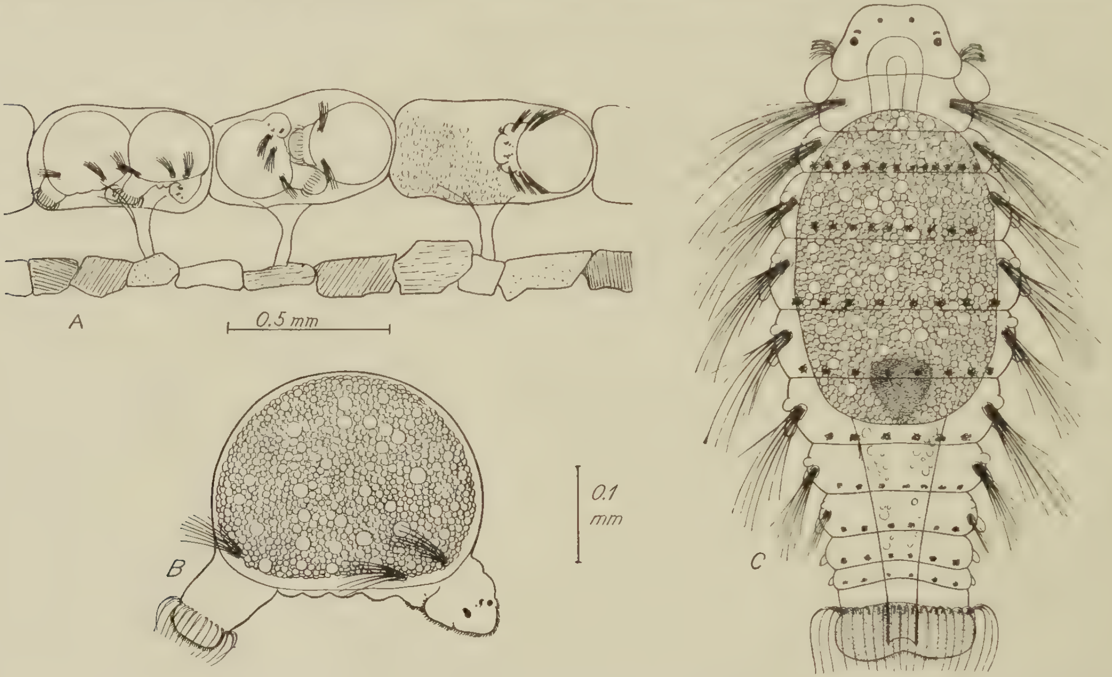


Fig. 40 A-C. *Pygospio elegans* Claparède. Egg capsules and embryos caught off Julebæk, depth $^{1}/_{2}$ m, on $^{16}/_{7}$-1945 and drawn from life on the day of capture. — *A*. Section of an egg string dissected out of the tube of the mother animal. Each capsule adheres by a slimy thread to the dissected tube wall. Two capsules with two embryos and one capsule with one embryo and nurse eggs in dissolution are seen. The embryos were all of the hunch-backed type sketched in fig. 40 B (seen from the right side). — *C*. Old embryo approaching the more slender shape characteristic of the large pelagic larval type.

However, another type of Spionid larvae frequently met with in the plankton have also proved to belong to *Pygospio elegans*. In the spring of 1944 Mr. Erik Rasmussen continued his work to clear up the larval development of this species in the Isefjord. He found small 3-segmented larvae, still enclosed in capsules taken into the tubes of the mother animals. I had the opportunity to watch these larvae in a living state and found that they showed so close a similarity to a type of Spionid larvae extremely common in the Sound that these latter larvae could be referred without hesitation to *Pygospio elegans*. These larvae from the Sound had previously been supposed by me to belong to *Spio filicornis* (which see) because their three segments with long larval bristles agreed fairly well with Mesnil's description of the larvae of this species, and because they showed some similarity to quite young bottom-stages of *Spio filicornis* (cf. fig. 46 A-B), sketched by the present author in East Greenland. Now, however, they have distinctly proved to belong to *Pygospio elegans* and not to *Spio filicornis*, the pelagic larvae of the latter species being accordingly still unknown from Danish waters.

Thus, we are able to distinguish between the following main types of larvae from the Sound-plankton, all belonging to *Pygospio elegans*:

A. Small dark larvae with long larval bristles (no figures). Such larvae are 330 to 340 μ long, have three pairs of black eyes, ciliated "shoulders", and a distinct telotroch. The intestine, which is distinctly visible through the body wall, has a very solid wall. It may be yellowish-green to colourless, but it often exhibits a bluish-black pigmentation, which gives the larva a very dark appearance. The first chaetigerous segment is provided with very long provisional setae, and on even the slightest disturbance the larva will coil together with all its chaeta projecting like an angry hedge-hog. By far the majority of these larvae in the Sound have three to five chaetigerous segments only — a fact which proves that at least some of them originate from parents in the Sound proper. The oldest larvae found within a maximum of this small form have eight or probably nine chaetigerous segments. Their stay in the plankton seems thus to be rather short, and normally they will not develop into such large pelagic larvae as form the second main type in the Sound plankton.

Larvae of this type are known from plankton taken off Ven on: $^{9}/_{10}$-37 (2 spms.); $^{18}/_{12}$-37 (2 spms.); $^{5}/_{1}$-38 (18 spms.); $^{23}/_{1}$-38 (1 spm.); $^{3}/_{4}$-38 (12 spms.); $^{10}/_{5}$-38 (6 spms.); $^{18}/_{6}$-38 (3 spms.); $^{1}/_{7}$-38 (2 spms.); $^{4}/_{12}$-38 (7 spms.); $^{4}/_{3}$-39 (10 spms.); $^{25}/_{3}$-39 (about 35 spms.); $^{10}/_{4}$-39 (1 spm.), and $^{5}/_{8}$-39 (1 spm.), and off Helsingør on $^{17}/_{9}$-41 (4 spms.); $^{7}/_{10}$-41 (1 spm.); $^{25}/_{10}$-41 (1 spm.); $^{11}/_{11}$-41 (1 spm.); $^{2}/_{12}$-41 (7 spms.); $^{19}/_{12}$-41 (8 spms.); $^{3}/_{1}$-42 (4 spms.); $^{31}/_{1}$-42 (about 140 spms., several just hatched and still without black intestines; all transitional stages to somewhat older larvae with black intestines were found); $^{21}/_{2}$-42 (about 220 spms., mostly quite young); $^{21}/_{3}$-42 (about 120 spms. all with black intestines); $^{27}/_{4}$-42 (14 spms. in the eight-segment stage); $^{15}/_{5}$-42 (11 spms. in the eight-segment stage); $^{18}/_{7}$-42 (1 spm.), and $^{5}/_{9}$-42 (4 half-grown larvae). — Their maximum seems to occur in the late winter and early spring, while they are extremely rare in the summer.

B. Large, colourless larvae with short larval bristles (fig. 41 C-E). Such larvae are 1600—2300 μ long with 15 to 20 chaetigerous segments. The cilia on the "shoulders" as well as those of the telotroch have disappeared. The distinct intestine is normally unpigmented and has light olive-green contents; the pharynx and the lips are faintly reddish-brown, the pharynx with a brownish pigmentation along the dorsal side. All segments are provided with small grains of bluish-black pigment on the dorsal side. The anal segment has a yellowish-brown pigmentation on the dorsal and a greenish pigmentation on the ventral side with spots of black pigment at the terminal end. Near the anus the intestine is provided with black pigment. The anal segment shows similar fusiform, clear cells as are characteristic of several other Spionid-larvae. Three pairs of black eyes. Prostomium with a brownish pigmentation in front on the dorsal side.

Larvae of this type are known from plankton taken off Ven on: $^{19}/_{12}$-37; $^{6}/_{1}$-38 (43 spms.); $^{23}/_{1}$-38 (19 spms.); $^{3}/_{4}$-38 (112 spms.); $^{18}/_{4}$-38 (11 spms.); $^{6}/_{6}$-38 (222 spms.); $^{18}/_{6}$-38 (64 spms.);

$^{1}/_{7}$-38 (11 spms.); $^{24}/_{9}$-38 (1 spm.); $^{25}/_{3}$-39 (1 spm.); $^{10}/_{4}$-39 (12 spms.); $^{17}/_{5}$-39 (6 spms.); $^{4}/_{6}$-39 (3 spms.); $^{17}/_{6}$-39 (5 spms.); $^{3}/_{7}$-39 (6 spms.); $^{15}/_{7}$-39 (2 spms.), and off Helsingor on: $^{2}/_{12}$-41 (7 spms.); $^{19}/_{12}$-41 (10 spms.); $^{3}/_{1}$-42 (2 spms.); $^{31}/_{1}$-42 (5 spms.); $^{21}/_{2}$-42 (2 spms.); $^{21}/_{3}$-42 (5 spms.); $^{15}/_{5}$-42 (1 spm.); $^{18}/_{7}$-42 (15 spms.); $^{25}/_{7}$-42 (9 spms.), and $^{3}/_{4}$-45 (several spms.). – Thus, these larvae are abundant in the plankton from December to June-July, but seem to be totally or nearly absent in the late summer and autumn. Normally they seem to hatch in the 15-setiger stage, but occasionally they are closely associated with a maximum of smaller larvae, which form:

C. Transitional stages between the small and the large larval types (fig. 41 A, B). Such larvae are about 500–600 μ long, with 10–12 chaetigerous segments; they have 3 pairs of black eyes, a distinct dark-pigmented or olive-green intestine, dark-pigmented and yellowish-brown anal segment, dark-pigmented hindmost part of the intestine, ciliated "shoulders", distinct telotroch, long, provisional larval bristles on the first chaetigerous segments, and dark transverse spots of pigment along the dorsal side of each segment. Such larvae, which still show several of the characteristics of the 3- to 4-setiger larvae described under A, when carefully examined proved to form all transitional stages to the large larvae mentioned under B and shown in fig. 41 C-E, and during their pelagic life will, no doubt, grow and develop into larvae like these.

Larvae of this intermediate type are known from plankton taken off Ven on: $^{6}/_{1}$-38; $^{23}/_{1}$-38; $^{22}/_{12}$-38 (141 spms.); $^{7}/_{1}$-39 (21 spms.); $^{28\text{-}29}/_{1}$-39 (28 spms.); $^{25}/_{3}$-39 (10 spms.), and $^{10}/_{4}$-39, and off Helsingør on: $^{2}/_{12}$-41; $^{19}/_{12}$-41; $^{31}/_{1}$-42; $^{21}/_{2}$-42 (8 spms.), and $^{3}/_{4}$-45 (a few specimens). On other occasions they may, however, have been confused with larvae of the other two types. — Their occurrence seems mainly to be restricted to the winter and early spring.

In the Sound we may accordingly distinguish between three types of pelagic larvae all belonging to *Pygospio elegans,* viz. A. Small larvae with long larval bristles and dark-coloured intestines, which hatch in the three- to four-setiger stage and normally metamorphose in the eight- to nine-setiger stage still with an appearance very much like that which they had in the hatching stage, B. Large larvae with short larval bristles and light transparent colours, which normally hatch in the fifteen- to sixteen-setiger stage and leave the plankton with about 20 segments, and, finally, C. Intermediate stages, which closely resemble (dark colour, long bristles, ciliary rings) the small larvae of type A (and probably now and then may originate from such type-A larvae as have continued their pelagic life longer than usual) and at the same time show all transitional stages to the large larvae of type B, some of which undoubtedly originate from these intermediate stages.

These complicated conditions agree well with a couple of exceedingly interesting observations made by Mr. Erik Smidt at Esbjerg (SW. Jutland). Smidt, who has kindly allowed me to mention his results, in the plankton found three different types of pelagic Spionid larvae — differing in size, shape, bristles, and pigmentation. After having been thoroughly sketched, all three types were put into glass dishes (each type in its own dishes) where they all metamorphosed into *Pygospio elegans.*

How are we to explain these curious observations? The explanation is no doubt to be sought in the feeding habits in the egg capsule, viz. by nurse eggs. We know capsules with two larvae per capsule only (Julebæk, own observations, and the Isefjord, kind information by Mr. Erik Rasmussen), with three to five larvae per capsule (Aalsgaarde, own observations) and with seven to nine larvae per capsule (Bohuslän, according to Söderström 1920). As these larvae feed on nurse eggs, it seems likely that they will hatch at an earlier stage if seven to nine competitors

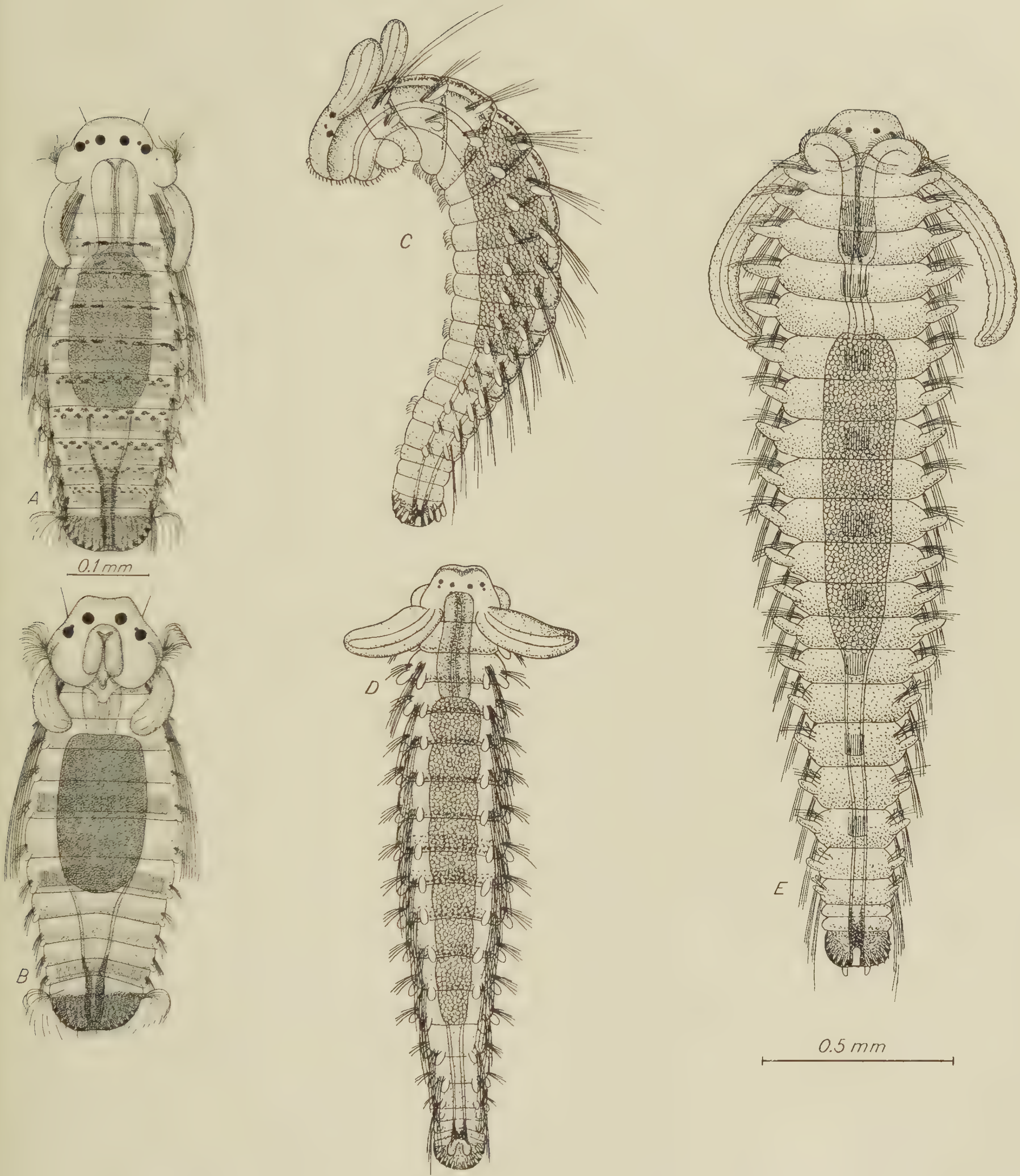


Fig. 41 A-E. *Pygospio elegans* Claparède. Larvae from plankton off Snekkersten, depth 8 to 0 m, caught and drawn from life on $^3/_4$-1945. — *A* and *B*. Larvae of medium size, seen from the dorsal side (A) and from the ventral side (B). (See the text p. 86). — *C* and *D*. Larvae in the 15-setiger stage (largest larval type, see the text pp. 85–86), seen from the dorsal side (D) and the left side (C). — *E*. Larva in the 20-setiger stage, i. e. the oldest planktonic larva found, seen from the ventral side.

have to live on a certain amount of nurse eggs than if for instance only two competitors have a similar amount of nurse eggs at their disposal. This probably provides the explanation of the different pelagic larval types. Larvae hatched early and exposed to the light and the free water masses in a younger stage will probably be much more pigmented and develop much stronger swimming setae than those hatched in an older stage etc. — The dark three to four setiger larvae occurring spontaneously in the plankton with large maxima, all of the same size and, when newly hatched, apparently with an empty intestine, may e. g. originate from embryos which have developed on their own contents of yolk without devouring nurse eggs; the large larvae of type B may originate from such hunch-backed embryos which, feeding on nurse eggs, will not hatch until all the nurse eggs have been devoured, and the larvae of intermediate shape and size may originate from embryos which have had to feed on nurse eggs together with so many competitors that the quantity of food at the disposal of the individual larva has been small as compared with that devoured by the large larvae of type B. — Finally it is to be expected that also a totally non-pelagic development may take place in this species, viz. when for instance a single larva has at times all the nurse eggs of a whole capsule at its disposal. — These remarks, however, should only be regarded as a hypothesis for future work on this species, which seems to be an extremely interesting object for further studies.

Larvae of this species, unlike most other planktonic bottom animal larvae, are photopositive even in the oldest planktonic stage, a fact which is in good agreement with the habitat of the adults, which is near the shore and the surface.

Polydora ciliata JOHNSTON. Extremely common in the Sound.

Reproduction: A. Literature. In the copious literature on *Polydora* larvae three papers are of particular interest, viz. those of LESCHKE (1903), SÖDERSTRÖM (1920), and, especially, that of WILSON (1928a), in which the whole development is described and figured and the earlier literature is discussed. A brief summary of these papers will be given here: Spawning season at Kiel from April to October, with a maximum in July, at Plymouth from January to October, with a maximum in March. The eggs are laid in transparent sacs, each of which is fused with its neighbours at either end, forming together a long string consisting of 15—20 sacs. These strings are attached to the inner wall of the burrow (each sac anchored by two filaments). Each sac contains from 15—20 eggs (WILSON) to 70—80 eggs (SÖDERSTRÖM), each egg being 130–140 μ across, opaque, and densely granular with yolk. The larva hatches in the three-setiger stage and will not leave the plankton until reaching a stage with 18 chaetigerous segments. Fine figures of all larval stages are given by WILSON (l. c. pl. I—IV). — The typical specialised bristles of the fifth segment are only conspicuous in the old larvae, but the faintly yellowish colour of the larva and its characteristic pattern of black pigment makes the *Polydora* type easily recognisable in the plankton. WILSON (l. c.) compares the pelagic stages of *P. ciliata* and *P. hoplura*, mentioning differences in the number of segments, pigmentation, etc. His comparison shows the following characteristics of the *P. ciliata* larva: hatching in the three-setiger stage, pelagic until the eighteen-setiger stage. After the formation of the vestibule the majority of larvae of all stages have a mass of pigment, often dark-brown or black, at the corners of the cheeks. Only a little brown (later black) pigment is seen in the anal region. The late-stage larvae have two rows of black chromatophores along the back. The chromatophores between the two pairs of eyes characteristic of *P. ciliata* as well as of *P. hoplura* are lacking in other species of *Polydora* larvae. — HOFKER mentions ripe specimens, egg capsules, and free swimming larvae from den Helder (Holland) in May, the youngest of them with four chaetigerous segments (1920—22, p. CLXI), and the same author mentions and figures (1930, p. 195—98) larvae from the Zuidersee, where they occur all the year round with a maximum in the summer (smallest larvae here have five chaetigerous segments).

B. Own remarks. As mentioned above, *Polydora ciliata* is extremely common in the Sound, where it inhabits mollusk shells and — in the southern part of the Sound — the limestone exposed at the bottom. An examination of 82 shells of living *Littorina littorea* from Aalsgaarde, taken at a depth of 1 m, on $^{24-25}/_{6}$-41, proved that 47 of these shells, i. e. 57 per cent, contained living specimens of *Polydora ciliata.* Fourteen of the shells contained from 10—100 living specimens of *Polydora* each. Observations from Helsingør and Ven seem to confirm this high frequency of the species, which is, no doubt, the commonest Polychaete in the Sound. On $^{4}/_{7}$-41 three shells of living *Littorina littorea* (taken off the point of Kronborg, at a depth of 10—20 m) highly infected with *Polydora ciliata* were broken by means of a hammer, and the tunnels were found to contain a large number of living specimens of *Polydora,* several of them with egg-strings. While some of these egg-strings contained slightly developed eggs only, others were filled with larvae ready to hatch. A large number of such larvae hatched during the observation and swam readily about in the water. They had three chaetigerous segments, and their pigmentation agreed in all details with that found by WILSON (l. c.) at Plymouth. Also *Polydora ciliata* larvae from the harbour of Copenhagen, reared and sketched by Mr. ERIK RASMUSSEN in September 1941, agree closely with WILSON's drawings. Thus the larvae from the Sound seem to agree closely with those figured from Plymouth, and accordingly the main part of the *Polydora* larvae from the Sound should be referred to *Polydora ciliata.* The larvae (fig. 42 A-C) are so well described by WILSON (l. c.) that it seems unnecessary to describe them here.

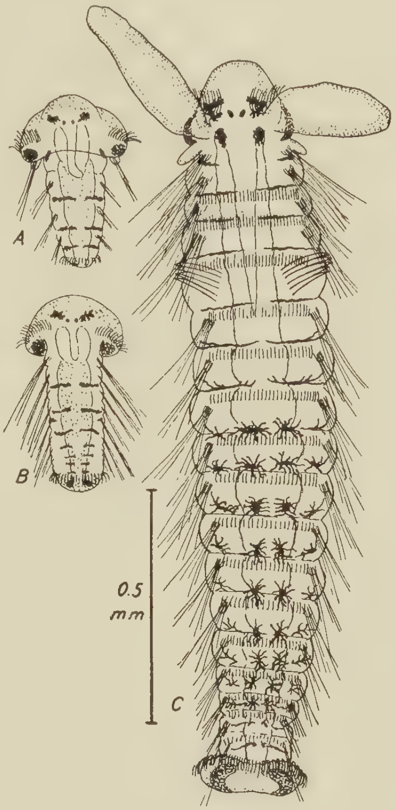


Fig. 42 A-C. *Polydora ciliata* JOHNST.— *A* and *B*. Young larvae from plankton, taken off Ven, depth 14 m, on $^{22}/_{8}$-1937, rough sketches only, drawn from life on $^{13}/_{8}$-1937. — *C*. Older larva from plankton off Ven, caught and drawn from life on $^{5}/_{8}$-1938. The bristles on segment 5 are distinct. The pigmentation round the eyes, on the cheeks, and along the back are characteristic of the species.

In our four-year samples such larvae are present, taken off Ven on the following dates: August 1936; $^{12-13}/_{9}$-36; $^{6}/_{12}$-36; $^{19}/_{12}$-36; $^{9-10}/_{1}$-37; in February to May 1937, insufficient observations; $^{21}/_{6}$-37; $^{2}/_{8}$-37; $^{6}/_{8}$-37 (about 1600 spms.); $^{9}/_{8}$-37 (763 spms.); $^{12-13}/_{8}$-37 (7000 spms.); $^{12}/_{9}$-37; $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{23}/_{10}$-37; $^{5}/_{12}$-37; $^{18}/_{12}$-37; $^{16}/_{2}$-38 (about 1900 spms.); $^{12}/_{3}$-38; $^{3}/_{4}$-38; $^{18}/_{4}$-38; $^{22}/_{5}$-38 (about 2150 spms.); $^{6}/_{6}$-38 (about 1450 spms.); $^{17}/_{7}$-38; $^{13}/_{8}$-38; $^{11}/_{9}$-38 (3 spms.); $^{12}/_{11}$-38 (6 spms.); $^{7}/_{1}$-39 (1 spm.); $^{30}/_{4}$-39 (700 spms.); $^{17}/_{5}$-39 (about 100 spms.); $^{4}/_{6}$-39; $^{17}/_{6}$-39 (about 100 spms.); $^{3}/_{7}$-39; $^{15}/_{7}$-39; $^{5}/_{8}$-39 (1 spm.); $^{18}/_{8}$-39 (3 spms.); $^{16}/_{9}$-39 (1 spm.), and off Helsingør on: $^{17}/_{9}$-41 (4 large spms.); $^{7}/_{10}$-41 (3 large spms.); $^{25}/_{10}$-41 (3 large spms.); $^{11}/_{11}$-41 (1 spm.); $^{2}/_{12}$-41 (2 half-grown spms.); $^{19}/_{12}$-41 (1 large spm.); $^{31}/_{1}$-42 (1 large spm.); $^{21}/_{2}$-42 (70 young larvae); $^{21}/_{3}$-42 (15 young larvae); $^{27}/_{4}$-42 (16 young and half-grown larvae); $^{15}/_{5}$-42 (17 half-grown and large larvae); $^{4}/_{6}$-42 (1 large larva); $^{20}/_{6}$-42 (12 large larvae); $^{6}/_{7}$-42 (2 young larvae); $^{18}/_{7}$-42 (32 mostly large larvae), and $^{25}/_{7}$-42 (10 larvae). Near Ven the larva is a spring- and summer-form, which normally has its main occurrence from April to September, when the species dominates totally among the Polychaete larvae in the plankton. A large spawning may exceptionally take place outside this season, thus for instance on $^{16}/_{2}$-38 (larvae from this date were carefully sketched when alive and are typical *ciliata* larvae). All stages are found in the plankton, the late larvae being almost just as frequent as the young. It would seem that the waste of larvae during the pelagic life is rather small, a fact which is probably accounted for by the omnivorous tendency of the larvae. Besides feeding on phytoplankton (as stated by Wilson, l. c.), they are able to swallow larvae of Lamellibranchs and other pelagic microorganisms. They are very voracious and seem to have a rather long pelagic life. In the harbour of Copenhagen larvae of *Polydora ciliata* are present in the plankton from May to September, often in large numbers (see Smidt 1944, p. 256).

Polydora coeca Ørsted. Southern part of the Sound, very common. Northern and middle parts, rather rare.

Reproduction: A. Literature. The reproduction of this species is unknown, while it is well known for *Polydora ciliata* (see above), and *Polydora hoplura* (larvae feeding on nurse eggs will not hatch till 12 chaetigerous segments and the tentacles have developed; pelagic stage somewhat shortened, Wilson 1928 a); the egg capsules are known for *Polydora ligni* (laid singly in the tube of the mother animal, Söderström 1920), *Polydora commensalis,* and *Polydora polybranchia* (egg capsules in the tube of the mother animal, Mesnil 1916). Finally, *Polydora natrix* (Söderström 1920) seems to nourish its young on dissolving muscles in the hindmost, epitoquous segments of its body, which will "die" and form a "breeding capsule" round the young, which — when hatching — have at least 19 chaetigerous segments. Egg-capsules placed in the tube of the mother animal and eggs which develop in a long or somewhat reduced pelagic stage are, however, the rule for most species within the genus *Polydora.*

B. Own remarks. Besides the dominant larvae of *Polydora ciliata,* another *Polydora* larva is also very frequent in the Sound. In our samples this larva was taken off Ven on the following dates: $^{19}/_{2}$-39 (about 1000 spms.); $^{4}/_{3}$-39 (6400 spms.); $^{25}/_{3}$-39 (about 1300 spms.); $^{10}/_{4}$-39 (8 late larvae), and $^{17}/_{5}$-39 (2 late larvae), and off Helsingor on: $^{21}/_{3}$-42 (about 900 larvae, most of them with 10—15 chaetigerous segments, a few with 18 chaetigerous segments, 4 larvae had large *Coscinodiscus* in their stomachs); $^{10}/_{4}$-42 (13, all ready to metamorphose); $^{27}/_{4}$-42 (7 ready to metamorphose); $^{15}/_{5}$-42 (1 large larva); $^{20}/_{6}$-42 (2 half-grown larvae); $^{17}/_{8}$-42 (1 large and 1 half-grown larva), and $^{5}/_{9}$-42 (a large larva). The larvae seem, thus, to have a maximum in February and March. During this season they are extremely common and must accordingly belong to a species of *Polydora* which is frequent in the Sound. As, furthermore, the larvae were present in all stages with from 7 to 18 chaetigerous segments, they must originate from the nearest vicinity. Larvae of this type are rather common in the plankton in the harbour of Copenhagen in March to April. As *Polydora coeca* is common in the adult stage in the southern part of the Sound, and as *Polydora quadrilobata* — the third species of *Polydora* known from the Sound — is mentioned as "rare" by Eliason (l. c.), our larvae must be referred to *Polydora coeca.* The late larva with 18 setigers (fig. 43) and 1760 μ long is very characteristic and can easily be distinguished from larvae of *Polydora ciliata* in a similar stage. The larva of *P. coeca* has no pigment at the corners of the cheeks, but brownish-black pigment in front of the eyes, no chromatophores between the eyes, a brownish-black line of pigment along the whole back, and above this two black chromatophores behind each other on each segment. Black pigment spots in front of the parapodia, and black transverse lines marking the boundaries between the segments. A dark-brownish black anal segment with black pigmentation. The specialised bristles on the fifth segment are shaped like a spoon. — The young larvae have not been sketched. The larva is a typical winter-form (in contrast to that of *Polydora ciliata*) and has its main occurrence in February to April (May).

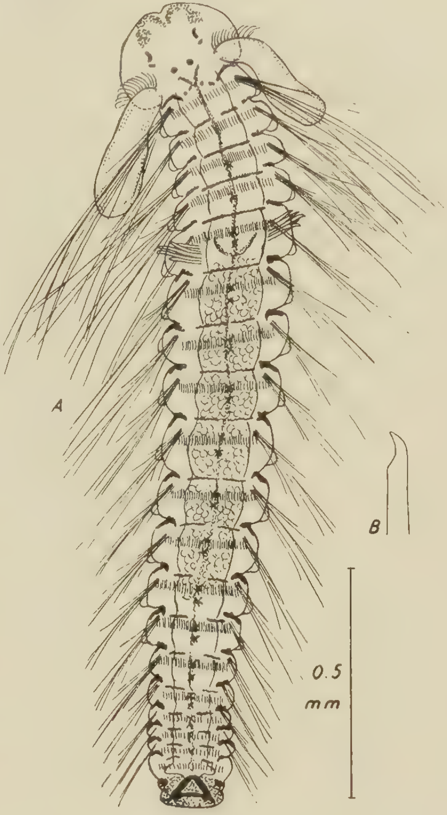


Fig. 43. *Polydora coeca* Ørsted. *A*. Old larva from plankton off Ven caught and drawn from life on $^{4}/_{3}$-1939. The drawing was cheked by comparison with several other larvae taken off Helsingør on $^{21}/_{3}$-1942 and was found to be correct in all details. Younger larvae down to 7 or 8 segments were seen, but not sketched. — *B*. Spoon-shaped bristle from segment no 5 (not lancet-shaped as in *Polydora ciliata)*.

Polydora quadrilobata Jacobi. Middle and southern parts of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound. See the remarks under *Polydora coeca*.

Spiophanes bombyx (Claparède). Northern and middle parts of the Sound, rare.

Reproduction: A. Literature. McIntosh (1915, mgr., p. 185) says that "specimens procured on June the 15th had large ova. A female on May 22nd had a greater part of its body distended with greyish or dull yellow ova . . . . . (pl. 96, fig. 14) . . . . .". Claparède (1870) states that the ova are flattened spheroids, longest diameter 130 μ. McIntosh (l. c. pl. 94, fig. 16) figures a larva which he refers with some doubt to *Spiophanes bombyx*. The larva has 23 setigers, it is quite colourless with two pairs of eyes, two tufts of prototroch cilia, and two small tentacles. Two younger larval stages (McIntosh l. c., pl. 93, figs. 8—9) are likewise supposed by McIntosh to belong to *S. bombyx*. They are yellowish-colourless, with two and three pairs of eyes respectively. — Mesnil (1896, pp. 249—57) has examined the larvae of this species at Wimereux, where they are frequent from early June till late in August. Pelagic larvae from the 9-setiger stage to the 25-setiger stage were easily kept alive in glass dishes placed in the dark. They are characteristic by the total absence of black pigment, while yellow and orange pigment spots are found on the prostomium and around the telotroch. Two pairs of orange-red eyes and one pair of brown pigment spots, which are easily taken for eyes. During their stay in the glass dishes long antennae were developed. Mesnil (l. c. pl. 15, figs. 23—25) figures a larva with eight chaetigerous segments and very small tentacles, and a prostomium with larger tentacles of a late larva which had already the two frontal tentacles typical of the whole genus *Spiophanes*.

B. Own remarks. In a plankton haul taken off Ven, 18—0 m, on $^{5}/_{8}$-42, three larvae were observed (fig. 44 B), which by their distinct frontal tentacles could easily be referred to the genus *Spiophanes*. As, furthermore, the colour, number, and position of the eyes, and especially the colourless body with the total absence of black pigment, and the yellow and orange pigment round the teletroch, agree in all respects with the description given by Mesnil, I have no hesitation in referring the larva to *Spiophanes bombyx*. The larva was rather common in Ven-plankton in August 1944, but was never observed in our four years' regular main series; a few scattered specimens may, however, have been overlooked. The larva in question (fig. 44 B) is 1800 μ long, and has 22 chaetigerous segments. The prototroch is still active, and a transverse band of short cilia is seen on the dorsal side of each chaetigerous segment, while no ciliary ring was present on the anal segment. The eyes are carmine-coloured, a very pale dark-brown pigment is seen on the back, and the anal segment has yellow and orange pigment with a small black spot dorsal to the anus. From Frederikshavn (NW. Kattegat) several young larvae, which seem to be younger stages of the same species, are present; they were taken in a plankton haul, 26—0 m, on $^{29}/_{7}$-39. These larvae (fig. 44 A), 1300 μ long and with 18 chaetigerous segments, are also nearly colourless apart from the red eyes and the yellowish-brown anal segment; they have distinct frontal tentacles, and closely resemble the figure of the older *Spiophanes bombyx* larvae given by Mesnil (l. c. pl. 15, fig. 25). There is a pale yellowish-brown line along the back from a little behind the central pair of eyes to the anal segment.

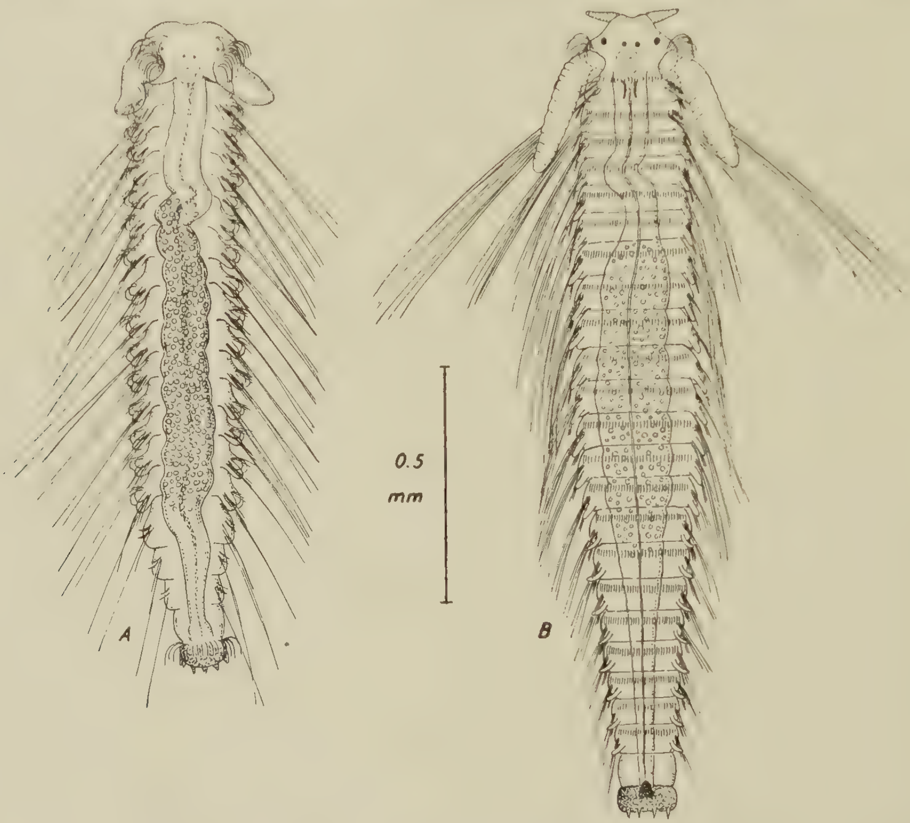


Fig. 44 A-B. *Spiophanes bombyx* (Claparède).—*A*. Medium-sized larva from plankton off Frederikshavn, NW. Kattegat, depth 28 to 0 m, caught and drawn from life on $^{29}/_{7}$-1939; seen from the dorsal side.—*B*. Old larva seen from the dorsal side. From plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{5}/_{8}$-1942.

Spiophanes krøyeri Grube. Northern part of the Sound, not rare.

Reproduction: A. Literature. Nothing is stated in the literature about the development of this species, while the larva of the closely related *Spiophanes bombyx* is well known (see above).

B. Own remarks. On $^{26}/_{8}$-38 three small larvae were found off Ven, which may probably be referred to this species (fig. 45). They were all of the same size, 620 μ long, with 6 chaetigerous segments, and had very long antennae, a feature which is mentioned by MESNIL (1896) as characteristic of young larvae of the related *S. bombyx* (see above), and which is probably characteristic of the whole genus *Spiophanes*. The larvae agree also with MESNIL's description of the *S. bombyx* larva in having two pairs of orange-coloured eyes and one pair of reddish-brown pigment spots resembling eyes, and in having orange-red and yellow pigment on the tentacles, the prostomium, and the anal segment. They differ, however, from MESNIL's description by having black transverse bands of pigment on five of the body segments. Accordingly it seems justifiable to refer the larvae to another species of *Spiophanes*, viz. *S. krøyeri*, but nothing definite can be stated. The drawing, though correct in the main features, should only be regarded as a rough sketch.

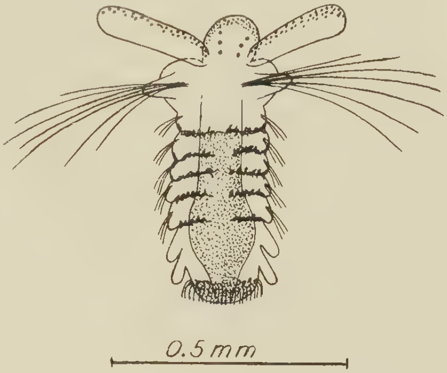


Fig. 45. Larva presumably belonging to *Spiophanes krøyeri* GRUBE (rough sketch, see the text pp. 93). From plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{26}/_{8}$-1938; seen from the dorsal side. Drawn by Mr. ERIK SMIDT.

Microspio arctica SÖDERSTRÖM. Taken by G. THULIN in the Sound, according to SÖDERSTRÖM (1920, p. 251).

Reproduction: A. Literature. Nothing is known concerning the reproduction of this species. CLAPARÈDE & METSCHNIKOFF (1869), however, have described the development of the closely related *Microspio Mecznikowianus* CLPRD. Their results are as follows: The sperms are contained in spermatophores. The females spawn in their tubes, and the eggs and larvae seem to be attached to the mother animals. Such larvae, figured by the authors cited above (plate XII, fig. 2 C), are telotrochous, with a distinct oesophagus, and with four pairs of eyes. They are hunch-backed, rich in yolk, and habitually they closely resemble that larval type of Nereids and of *Pygospio elegans* which develops without any planktonic stage. The same probably applies to *Microspio Mecznikowianus*.

B. Own remarks. Nothing is known about the reproduction of *M. arctica* in the Sound, but as the closely related *M. Mecznikowianus* has a non-pelagic development, similar features may be expected in *M. arctica*, which has its main distribution in arctic seas, where a pelagic development — as is well known — is extremely rare.

Spio filicornis O. F. MÜLLER (= **Spio martinensis** MESNIL). Rather common, especially in the middle and northern parts of the Sound.

Reproduction: A. Literature. MESNIL (1916) and MESNIL & CAULLERY (1917) have studied the reproduction and development. Their results are as follows: The adults live in compact sand, where they form fragile tubes badly stuffed with a thin, slimy membrane. The egg-masses, which often adhere to these tubes, are of two different types, viz. type A, especially common in April: straw-yellow egg-tubes 10—16 mm long with yellow eggs, 150 μ across, which hatch as pelagic larvae with 3 chaetigerous segments, — and type B, especially common in August: egg-tubes 10 mm long, of the same shape as type A, but whitish in colour and filled with eggs, which are only 130 μ across. The eggs in the egg-tubes are divided into smaller groups each consisting of 6—12 eggs surrounded by a membrane. Some of these eggs will break up into nurse-eggs, and the older embryos are found to have nurse-eggs as well as smaller embryos in their stomachs. The larvae hatch in the crawling stage with 15 chaetigerous segments and without the long larval bristles so well known in pelagic Spionid larvae. The pelagic larvae, which hatch from egg-tubes of type A, are 300 μ long, 130–140 μ broad, with 3 pairs of eyes, ciliated "shoulders", two white spots of pigment in the transitional area from the prostomium to segment 1, 3 pairs of chaetigerous segments, and long larval bristles. The intestine has a sulphureous pigment, and four small processes around the anus indicate the budding anal cirri. Egg masses of type A are figured, while no figures are given of type B and the larvae.

B. Own remarks. The brief description of the larva given by Mesnil (1916) seems only to refer to the larva just hatched, which has not yet taken any food from the plankton. The older pelagic stages are still undescribed, and so far no larva of *Spio filicornis* has been figured. — During a stay in Scoresby Sund (East Greenland) in the summer of 1933 I sketched some young bottom stages (fig. 46 A-B) taken in large numbers by means of Dr. Mortensen's detritus-sampler (Mortensen 1925) near Cape Hope, at a depth of 6 m, on a hard sandy bottom. I referred these larvae to *Spio filicornis*, which was very common in adult stages on the sand, and which is the only Spionid hitherto recorded from East Greenland (cf. Ditlevsen 1911, 1914). The larvae from Scoresby Sund have 13—15 chaetigerous segments; they have lost their larval bristles, and are in the crawling stage. They have three pairs of eyes, ciliated "shoulders", and a bluish-black pigmentation (or contents?) of the intestine. — The larval type fig. 41 A-B, which bears some resemblance to the East Greenlandic bottom-stages of *Spio filicornis*, and was first referred by me to this species, proved later on to belong to *Pygospio elegans* (cf. pp. 84 to 85); the pelagic larvae of *Spio filicornis* are still unknown from the plankton in the Sound and other Danish waters.

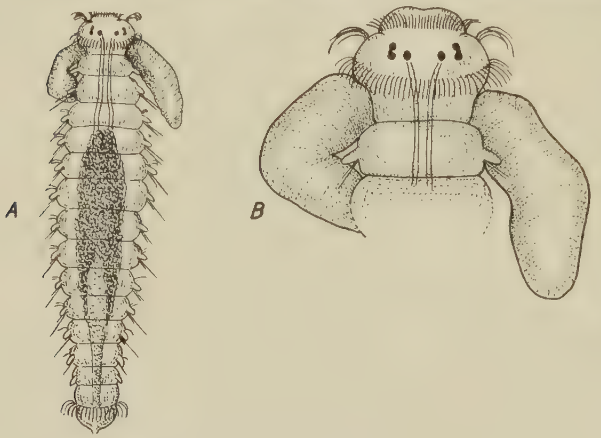


Fig. 46 A-B. *Spio filicornis* O. F. Müller. Larvae crawling near the bottom, taken with Mortensens' detritus sampler on the sand bottom, depth 6 m, off Cape Hope, Scoresby Sound, East Greenland, on $^{2}/_{7}$-1933 (drawn from life same day. No magnification was noted). As *Spio filicornis* was common in this locality and is the only Spionid known from East Greenland, the identity seems certain. — *A*. The whole larva, seen from the back. — *B*. Front part of the same larva, seen from the back.

Prionospio malmgreni Clap. Northern part of the Sound, probably not uncommon.

Reproduction: A. Literature. Lo Bianco (1899, p. 490) has seen ripe animals of this species in July, and small larvae taken in surface-plankton in August—September and kept in the laboratory metamorphosed into young of this species. Larger larvae were found by the same author in surface-plankton near the coast in September-October. However, the larvae have neither been described nor figured. Fewkes (1883, pl. I, figs. 1—13) described and figured different stages of larvae, which he referred to *Prionospio tenuis* Verr. Giard (1886) and Cerruti (1910), however, state that the larvae described by Fewkes should be referred to *Magelona papillicornis*, not to *Prionospio tenuis*. Finally, Cerruti (1910, no figures) has described the larva of *Prionospio* (species unknown) from Naples. Planktonic larvae with up to 50 chaetigerous segments may be found. In older larvae (from 22 to 50 segments) there is a distinct difference between the type of segments in the front part and in the hindmost part of the body; the tentacles are long and have a faintly flattened dilatation at their base, and the first pairs of gills with lateral papillae are developed. The prostomium is roughly triangular in front; four eyes are present.

B. Own remarks. Nothing is known about the reproduction in the Sound, and no larvae are known from the Sound plankton which can be referred to *Prionospio*.

Streblospio shrubsolii (Buchanan). Found in several specimens in the South Harbour of Copenhagen (kind information by Mr. Erik Rasmussen).

Reproduction: A. Literature. Hofker (1930, pp. 194—95) has described and figured larvae of the Spionid type from the Zuidersee which should probably be referred to *Streblospio dekhuyzeni* — a species which according to Fauvel (1927, p. 107) can hardly be distinguished from *S. shrubsolii*. The larvae, which occurred in large numbers, are 285 μ long, with 7—9 chaetigerous segments. They are telotrochous, short, broad and compact in shape, with two pairs of eyes (the larger of them nearest the margin); characteristic large cells form the base of the anal ciliary ring. Anal segments with green pigment, which also forms transverse bands on the dorsal side of each segment. The secondary setae, which — together with the primary setae — occur on the 8th and the following segments, agree closely with those described in the adult *Streblospio*. — While Buchanan, McIntosh, and Horst regard the genus *Streblospio* as a Spionid-genus, it is placed by Söderström and Fauvel among the *Cirratulidae* (cf. Fauvel 1927, pp. 106—107). If Hofker is right in referring the larvae to *Streblospio*, this genus must belong to the *Spionidae*, as the Cirratulid-larvae hitherto known are of an entirely different larval type (cf. *Audouinia tentaculata* (Wilson 1936), and *Aud. filigera* (Claparède & Metschnikoff 1869)). This was already pointed out by Wilson (1936).

B. Own remarks. Nothing is known about the reproduction of this species in Danish waters.

Other Spionid Larvae from the Sound.

In addition to the Spionid larvae already dealt with in this paper, six more larval species are of rather common occurrence in the Sound. To all appearance these larvae cannot be referred to any Spionid species hitherto known from the Sound in the adult stage.

Spionid larva A (fig. 47). Quite young larvae as well as larval stages with from 7 (560 μ long) to 13 (1130 μ long) chaetigerous segments are known from our plankton series. The larva is broad, with a short, broad prostomion and short, broad tentacles. Two pairs of eyes, the innermost of them red, the outermost black. The pharynx is black-pigmented, and the distal ends of the broad tentacles have often a brim of black pigment (not in the specimen figured here). The intestine is yellowish-brown in direct light, brownish-black in transmitted light. The apical ring of cilia is divided into two parts. Transverse bands of cilia on the ventral side of each chaetigerous segment, but not on the dorsal side. The identity of this larva is completely unknown. The larva is present in our samples taken off Ven on: $^{18}/_{4}$-38 (2 spms.); $^{22}/_{5}$-38 (4 spms.); $^{7}/_{1}$-39 (1 spm.); $^{4}/_{3}$-39 (1 spm.); $^{25}/_{3}$-39 (10 spms.); $^{10}/_{4}$-39 (1 spm.); $^{30}/_{4}$-39 (3 spms.); $^{17}/_{5}$-39 (2 spms.), and off Helsingør on: $^{17}/_{9}$-41 (2 spms.); $^{7}/_{10}$-41 (2 spms.); $^{31}/_{1}$-42 (20 spms.); $^{21}/_{2}$-42 (4 large spms.); $^{21}/_{3}$-42 (8 spms. in all stages), and $^{18}/_{7}$-42 (1 young spm.). Thus larvae occur from January to October with their main occurrence in January to April.

Spionid larva B (fig. 48 A-B). Larvae with 10 (830 μ long) to 12 or 13 (about 1300 μ long) chaetigerous segments found in the plankton. As shown in the figures, their appearance is very variable, and from the outset I have regarded them as two separate species. Observations on living larvae, however, have convinced me that they all belong to one and the same species, the differences in pigmentation being due to the dilated or contracted black chromatophores. The shape of the larva is broad, the intestine and its contents are colourless (apart from the black pigmentation often seen in the rectum). Two pairs of black eyes with pigment spots between. The black chromatophores on the back of the first chaetigerous segments form a figure resembling a spider. Yellow pigment (in direct light) is often found on the prostomium and on the anal segment. The identity of this larva is quite unknown. It has been found in plankton hauls from Ven taken on: $^{21}/_{8}$-38 (1 spm.); $^{26}/_{8}$-38 (3 large spms.); $^{29}/_{8}$-38 (1 large spm.), and $^{16}/_{9}$-39 (4 spms., 3 of them large), and from Helsingor on: $^{17}/_{9}$-41 (1 spm.); $^{7}/_{10}$-41 (31 spms. in all stages of development); $^{2}/_{12}$-41 (1 spm.), and $^{5}/_{9}$-42 (3 young spms.); thus the larva mainly occurs in the late summer and autumn.

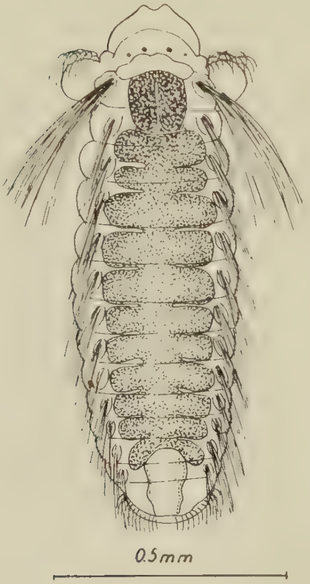


Fig. 47. *"Spionid larva A"*, the closer identity of which is unknown. Old larva from plankton between Hellebæk and Kulla Gunnarstorp, depth 30—0 m, on $^{17}/_{9}$-1941 (drawn from life on $^{18}/_{9}$-41). The distal end of the broad tentacles has often a black pigmentation which was absent from the specimen figured here.

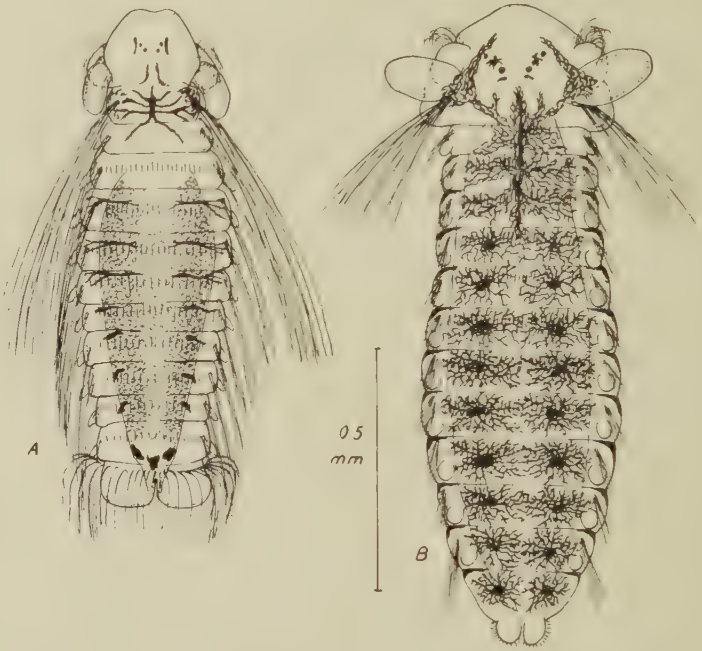


Fig. 48 A-B. *"Spionid larva B"*, the closer identity of which is unknown. — *A*. Larva of medium size with anal ciliary ring and with contracted chromatophores, showing the characteristic spider-like figure behind the head. Seen from the dorsal side. Taken from plankton off Ven, depth 18 to 0 m, on $^{16}/_{9}$-1939 and drawn from life the next day. — *B*. Older larva with extended chromatophores; the hindmost ciliary ring is reduced. Under the microscope the larva was slightly squeezed by the cover-glass and is therefore somewhat broader in the drawing than in nature. Also the long larval bristles had been thrown off before the animal was sketched. From plankton between Hellebæk and Kulla Gunnarstorp, depth 30 to 0 m, on $^{17}/_{9}$-1941 (drawn from life the next day).

Spionid larva C (fig. 49). Larvae about 1150 μ long with 14 to 15 chaetigerous segments, a broad body, three pairs of black eyes, with a small spot of black pigment between them. The larva is colourless with greyish-green granules in the intestine, greyish-brown pigment along the middle of the back, and yellowish-brown pigment at the front of the head and on the anal segment. Such larvae have been found in plankton samples from the following dates, taken off Ven: $^{6}/_{1}$-38 (2 spms.); $^{23}/_{1}$-38 (1 spm.); $^{6}/_{6}$-38 (1 spm.), and off Helsingør: $^{11}/_{11}$-41 (1 spm.); $^{10}/_{4}$-42 (130 spms.!, dominating larva); $^{27}/_{4}$-42 (15 large spms.), and $^{15}/_{5}$-42 (4 half-grown spms.). Thus larvae of this species are present in the plankton from November to June. Younger larvae have been found, too, so young that they seem to originate from parents in the neighbourhood. The large number of larvae from Helsingør taken on $^{10}/_{4}$-42 seems further to suggest that the parents are rather common in the Sound. Nevertheless the larvae have not yet been identified.

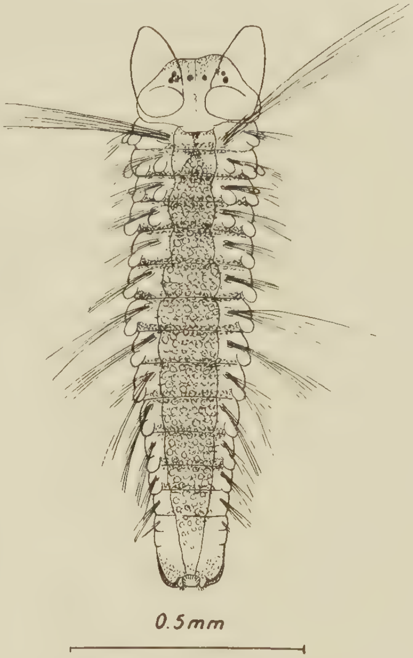


Fig. 49. *"Spionid larva C"*, the closer identity of which is unknown (see the text p. 97), Older larva from plankton between Hellebæk and Kulla Gunnarstorp, depth 35 to 0 m, taken on $^{27}/_{4}$-1942 (drawn from life on $^{28}/_{4}$-42).

Spionid larva D (fig. 50 A-D). Larvae differing from other Spionid larvae by having two lateral lobes with large cilia round the head. These lateral lobes, which together with the head form a small "umbrella", are provided with two rows of dark reddish-brown pigment spots, and a similar pigmentation is found on the whole anal segment. The larval body is yellowish transparent, the provisional capillary bristles of the first segment are very long, often longer than the whole body of the larva. In older larvae the ventral parapodia of the second chaetigerous segment bear no chaeta at all, the ventral parapodia of the third segment, however, bear only two specialised bristles, which resemble those characteristic of the fifth segment in *Polydora*. The ventral parapodium of the fourth and the following segments has capillary bristles. The tentacles are always of different size; normally the right tentacle seems to be the larger of them. Two pairs of black eyes. Larvae with 6 chaetigerous segments were 530 μ long, larvae with 8 chaetigerous segments 730 μ, and larvae with 19 chaetigerous segments 1180 μ. Larvae of this type were present in the Sound plankton taken off Ven on: $^{23}/_{5}$-37 (dominating Polychaete larvae in all stages of development); $^{10}/_{4}$-39 (5 spms.); $^{30}/_{5}$-39 (1 small spm.); $^{17}/_{5}$-39 (1 large spm.), and off Helsingør on: $^{27}/_{4}$-42 (19 spms. in all stages of development); $^{15}/_{5}$-42 (15 in all stages); $^{4}/_{6}$-42 (1 large spm.), and $^{18}/_{7}$-42 (1 large spm.), their occurrence being thus restricted to the period April-July. As mentioned above, these larvae differ in several respects from other Spionid larvae. They show some tendencies which remind one of the characters of the larvae of the *Sabellariidae* (cf. CAULLERY 1914, DRASCHKE 1885, and WILSON 1929) but they do not agree with these larvae either. Further, adult specimens of *Sabellariidae* are entirely unknown from the Sound, so the identity of these larvae still remains obscure.

Spionid larva E (fig. 51). Larvae 1080 μ long have 13 chaetigerous segments. The prostomium is broad with yellowish-brown pigment in front, with 3 pairs of black eyes, and with tufts of cilia on the sides. The foremost part of the intestine is yellowish-brown, the middle part greyish-green, and the hindmost part yellowish-brown. A dark brown ring of pigment on the anal segment. Dark lines of pigment form a V-shaped figure behind the eyes, cover the base of each parapodium, and form transverse lines on the dorsal side of the 6 hindmost segments. Tentacles broad and rather small. The most characteristic feature of the larva is the extremely long larval bristles — more than 1500 μ long or one and a half times the length of the whole larva. These long bristles are very easily thrown off, as for instance in the larva shown in fig. 51, which accordingly has only a minimum number of long bristles. — Such larvae were only observed in Helsingor plankton on: $^{17}/_{8}$-41 (1 large spm.) and $^{5}/_{9}$-42

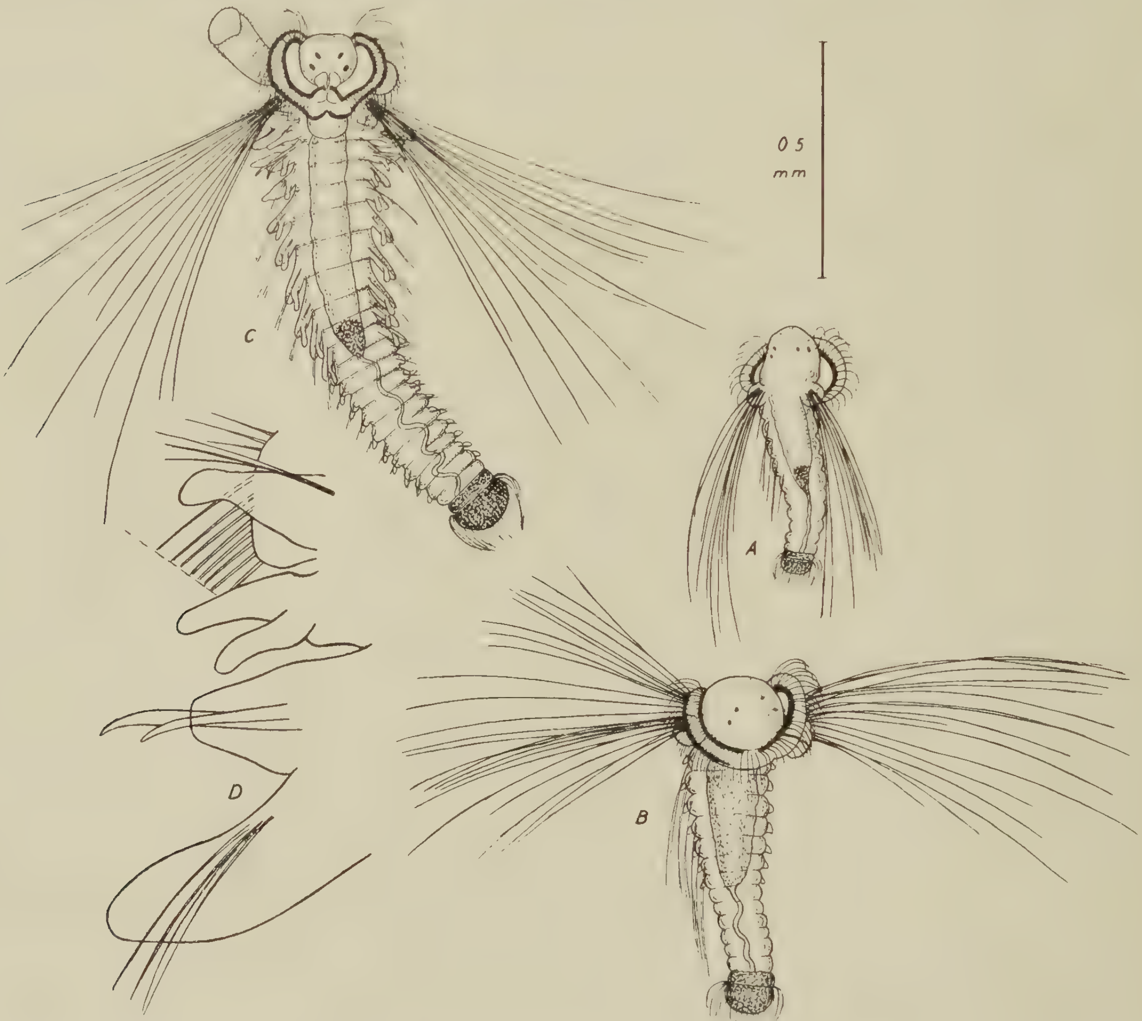


Fig. 50 A-D. "*Spionid larva D*", the closer identity of which is unknown (cf. the text p. 97). Larvae from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{10}/_{4}$-1939. — *A*. Larva with six chaetigerous segments; seen from the dorsal side. — *B*. Larva with eight chaetigerous segments; seen from the front and ventral side. — *C*. Larva with nineteen chaetigerous segments; seen from the ventral side. — *D*. The first four ventral parapodia from the right side of the larva shown in fig. C, more highly magnified. It is distinctly seen that segment II has no bristles at all, while segment III has specialised bristles resembling those on segment V of *Polydora*.

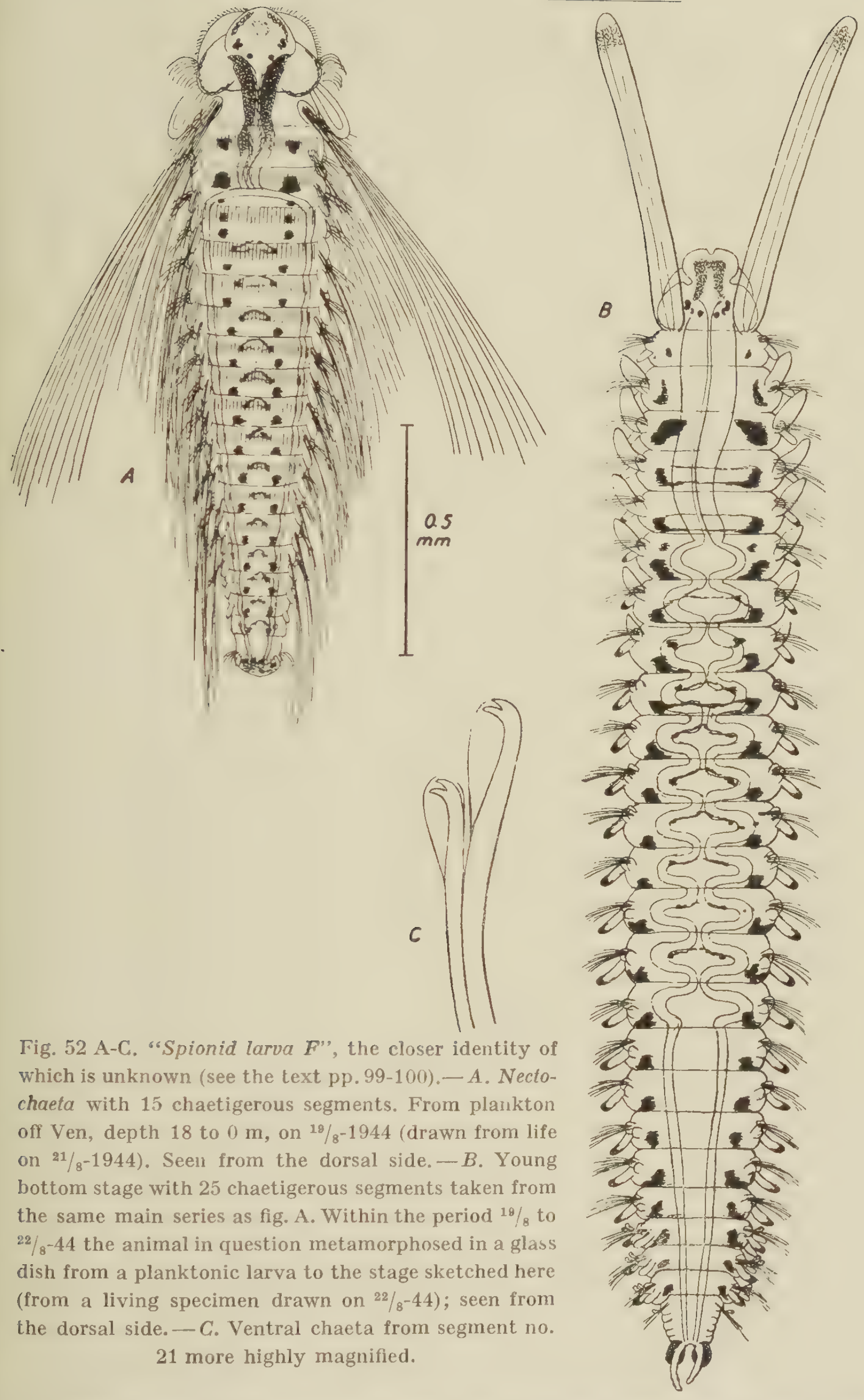


Fig. 52 A-C. "*Spionid larva F*", the closer identity of which is unknown (see the text pp. 99-100). — *A. Nectochaeta* with 15 chaetigerous segments. From plankton off Ven, depth 18 to 0 m, on $^{19}/_{8}$-1944 (drawn from life on $^{21}/_{8}$-1944). Seen from the dorsal side. — *B.* Young bottom stage with 25 chaetigerous segments taken from the same main series as fig. A. Within the period $^{19}/_{8}$ to $^{22}/_{8}$-44 the animal in question metamorphosed in a glass dish from a planktonic larva to the stage sketched here (from a living specimen drawn on $^{22}/_{8}$-44); seen from the dorsal side. — *C.* Ventral chaeta from segment no. 21 more highly magnified.

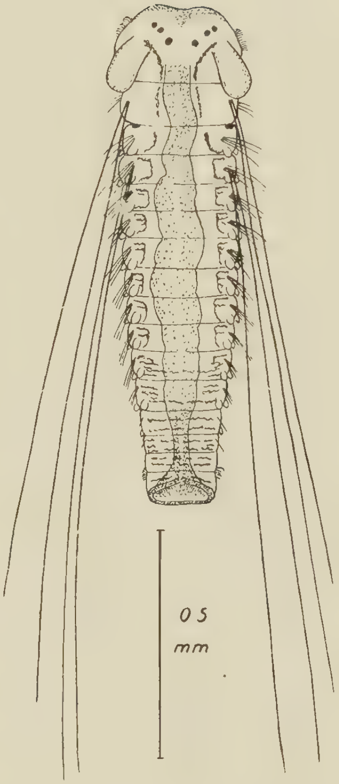


Fig. 51. "*Spionid larva E*", the closer identity of which is unknown (see the text pp. 97-99). Older larva from plankton between Hellebæk and Kulla Gunnarstorp, depth 30 to 0 m, on $^{5}/_{9}$-1942 (drawn from life on $^{6}/_{9}$-1942). Several of the provisional bristles had probably been thrown off before the animal was drawn.

(3 large spms.). Occasional specimens of the larva may have been overlooked in the Ven samples, but it seems altogether to be rare in the Sound. The identity is unknown.

Spionid larva F (figs 52 A-C). Larvae 1450 μ long (i. e. somewhat more than medium size) had fifteen chaetigerous segments. The rather broad prostomium had reddish-brown pigment along the margin in front and along the cheeks, a yellow spot of pigment anterior to the eyes, yellow pigment on the ventral side of the cheeks, and a deep black pigmentation of the pharynx; there is a characteristic black pigmentation on the dorsal side of all the segments, the black spots being largest on chaetigerous segments II and III. Brownish-black and lemon-coloured pigment on the anal segment. Three pairs of black eyes. Long provisional bristles on all segments. — Such larvae were found in a number of about ten per main series in the plankton off Ven, 18 to 0 m, on $^{19}/_{8}$-44. They had never been observed before in our main series, but may have been overlooked or confused with other Spionid larvae. — A still older larva from the same date and sample metamorphosed in a glass dish and was sketched in the young bottom stage on $^{22}/_{8}$-44 (fig. 52 B). It was then 2450 μ long (excl. of tentacles and anal cirri) and had 25 chaetigerous segments with hook-like ventral chaetae (fig. 52 C). The tentacles are long with a reddish-brown ring of pigment near the distal end; the prostomium has a characteristic reddish-brown pigmentation and the same three pairs of eyes as found in the planktonic stages. Also the black pigmentation along the back is as in the larva. The ventral cirri have black tips. —The identity of this larva and the young bottom stage is unknown.

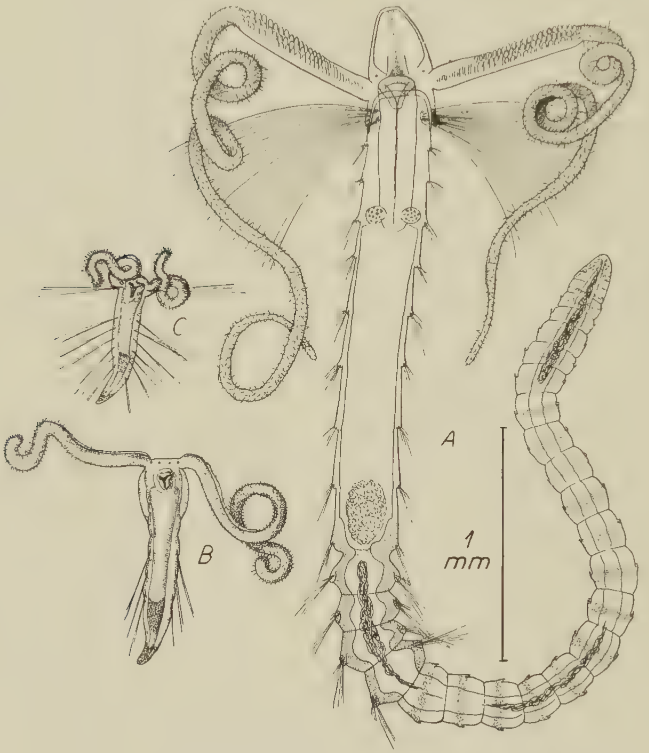


Fig. 53 A-C. *Magelona papillicornis* O. F. Müller. Larvae drawn from life. — *A*. Old larva, seen from the ventral side. Off Ven, plankton, depth 18 to 0 m, caught and drawn on $^{16}/_{8}$-1944. — *B* and *C*. Young larvae using their tentacles to move through the water. Both seen from the ventral side (rough sketches only). From plankton off Ven, depth 18 to 0 m, caught and drawn on $^{12}/_{7}$-1939.

Magelona papillicornis O. F. Müller. Fragments found in two localities in the northern part of the Sound. They belong to var. *rosea* Moore.

Reproduction: A. Literature. The larvae, described and figured by Fewkes (1883, pl. I, figs. 1—13) as *Prionospio tenuis*, have been referred to *Magelona papillicornis* by Giard (1886), Cerruti (1910), Flattely (1923, pl. III-IV), and McIntosh (1927), who (1878 and 1927) figures the ripe egg, 150 μ across, and states that the summer is the breeding season. The planktonic larvae, excellently figured by Fewkes (l. c.), have up to 33 chaetigerous segments. They are very characteristic. The thin body contains a very spacious intestine, which is often filled with larvae of Lamellibranchs. The first chaetigerous segment has long larval bristles. The tentacles are very long and muscular and are in constant motion. Being hauled through the water like lashes they are of fundamental value to the locomotion of the larvae. Four black eyes. Colour of larva: yellowish-red, transparent. — Hofker (1920—22, p. CLXII) states that these larvae are common in plankton off den Helder (Holland) in May, and adds that they feed on other worm larvae. Aiyar (1933, p. 115) describes and figures larvae of *Magelona* *papillicornis* from Madras (India). ALLEN (1915) records larvae from Plymouth in July-August-September, and FLATTELY (1923) larvae from Northumberland in July.

B. Own remarks. The *Magelona* larva (fig. 53 A-C) is present in our samples taken off Ven on: $^{19}/_{8}$-36; $^{26\text{-}27}/_{9}$-36; $^{24}/_{8}$-37; $^{12}/_{9}$-37; $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{17}/_{7}$-38; $^{21\text{-}26}/_{7}$-38; $^{5\text{-}13}/_{8}$-38 (very common); $^{27\text{-}28}/_{8}$-38; $^{11}/_{9}$-38; $^{3}/_{7}$-39; $^{13}/_{7}$-39; $^{15}/_{7}$-39; $^{5}/_{8}$-39, and $^{18}/_{8}$-39, and off Helsingør on: $^{25}/_{7}$-42 (5 spms.); $^{17}/_{8}$-42 (15 young spms.), and $^{5}/_{9}$-42 (4 half-grown spms.). Thus the larvae occur from July to October, with their maximum occurrence in August-September. In NW. Kattegat (Frederikshavn) larvae of this species were observed in the plankton on $^{26}/_{7}$-37. Usually they are only present in 2—5 spms. per 10 vertical hauls. More than 50 per cent of all the larvae found contained Lamellibranch larvae in their stomachs (especially larvae of *Mytilus edulis* — the dominant larval Lamellibranch in the summer); the number of Lamellibranch larvae which are devoured by the *Magelona* larvae in the Sound during the year is no doubt rather large.

Poecilochaetus serpens ALLEN. Adult specimens not recorded from the Sound. Larvae common in summer plankton.

Reproduction: A. Literature. ALLEN (1905) found ripe sexual products in adult animals in February, April, May, June, August, and December, i. e. the species breeds nearly all the year round. "The ripe eggs are lenticular in shape, the long diameter being about double the short". The longest diameter of the egg is about 200 μ, the protoplasm is concentrated in the centre, and the periphery of the egg contains similar vesicles as are known from the eggs of *Nerine cirratulus*, i. e. the egg is probably pelagic. The larva has been figured, discussed, and described by CLAPARÈDE (1863, p. 6, figs. 3 and 8, "larve indéterminée"), EHLERS (1874, correctly identified), GRAVELY (1909a, fig. 22, "Spionid A"), and FLATTELY (1923, pl. III). McINTOSH (1927) states that at St. Andrews larvae occurred in tow nets from June to October. Larvae occur during the summer at Plymouth (ALLEN 1915) and during July to September at Northumberland (FLATTELY 1923). The larva of *Poecilochaetus* is remarkable by retaining its pelagic habit until a late stage of development. It is 8 to 10 mm long, has a reddish-purplish colour with reddish-brown pigment just behind the head. The larva swims by means of rapid undulating movements of the whole body like those of a snake. The dorsal cirri and ventral cirri in the front part of the body are retort-shaped.

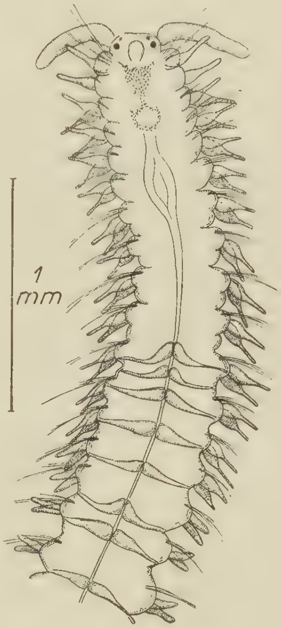


Fig. 54. *Poecilochaetus serpens* ALLEN. Front part of a larva with 42 chaetigerous segments, seen from the dorsal side. The pigmentation behind the prostomium is reddish-brown. From plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{8}/_{8}$-1938.

B. Own remarks. In spite of the fact that adult specimens have never been recorded from the Sound, the larvae are rather common in the summer plankton, where they always attract the attention because they are among the largest of all bottom animal larvae known from the plankton in this area. Fig. 54 shows the front part of a larva, which, when captured, had 42 chaetigerous segments. Larvae were found in plankton taken off Ven on: $^{8}/_{8}$-38 (1 spm.); $^{9}/_{8}$-38 (3 spms.), and $^{5}/_{8}$-39 (1 spm.), and off Helsingør on: $^{17}/_{9}$-41 (2 spms.); $^{17}/_{8}$-42 (5 spms., 3 of them young larvae, 2 older larvae of a deep purplish colour), and $^{15}/_{9}$-42 (1 young larva). They only seem to occur in the Sound in August to September. Off NE. Jutland (Frederikshavn) they have also been observed in plankton in July and August. Larvae with less than

30 segments have not been observed in our samples; so it is quite possible that larvae of this species found in the Sound are "drift-larvae", originating from parents which live in water areas far from the Sound.

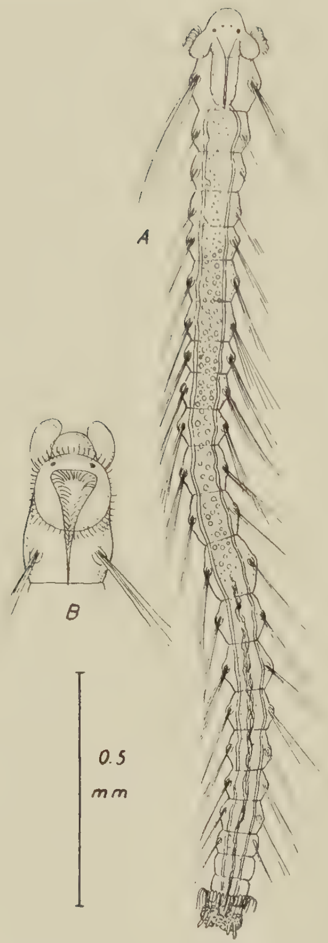


Fig. 55 A-B. Larva, presumably belonging to *Disoma multisetosum* ØRSTED, from plankton off Ven, depth 18 to 0 m, caught and drawn from life on $^{5}/_{8}$-1942. — *A*. Older larva seen from the dorsal side. — *B*. Head of old larva seen from the ventral side (rough sketch only, magnification unknown).

Disoma multisetosum ØRSTED. Common in the northern and middle parts of the Sound.

Reproduction: A. Literature. The reproduction and larval development of this animal, the type locality of which is the island of Ven, where the main part of our investigations were carried out, are totally unknown.

B. Own remarks. Adult specimens of *Disoma multisetosum* are very common in the Sound. As already mentioned, the larva is unknown, while the larvae of the other genus within the *Disomidae*, viz. *Poecilochaetus*, are well known (see above). If, therefore, we were to look for the larvae of *Disoma*, it might be expected beforehand that they would have a long pelagic life, would be very slender in shape, and would show close similarities to those of the *Spionidae* (to which the *Disomidae* are still referred by some authors). Considering our experiences from *Poecilochaetus* it is further probable that the *Disoma* larva differs from the Spionid larvae in the following characters: No long provisional larval bristles, rather short tentacles, and a slender shape. — Our plankton samples from the Sound, however, contain numerous larvae of an unknown species, which exhibit these characteristics, and which cannot be referred to any other species known from the Sound. It seems reasonable, therefore, to refer the larvae to *Disoma multisetosum*, but it must be remembered that the reference is only based on a provisional calculation of probabilities.

Larvae with 22 chaetigerous segments (cf. fig. 55 A) are 2000 μ long, larvae with 35 segments are 2100 μ long. They are very slender, colourless to whitish, with two pairs of brownish-black eyes and short Spionid-like tentacles. A large tuft of cilia is seen on either side of the prostomium in the 22-setiger larva, which has also a distinct and active telotroch. The anal segment with its styliform protuberances has a reddish-brown pigmentation. The pharynx is distinct and the triangular mouth is very large with cilia in constant motion. A transverse row of cilia was seen on the ventral side of each chaetigerous segment. — The larval bristles are short as compared with the length of the larva. The largest bristles (those on segment 1) are only 320 μ long. The 35-segment larva (fig. 55 B, rough sketch), has somewhat longer tentacles, and the dorsal and ventral cirri on the first three chaetigerous segments have commenced to appear.

In our samples such larvae are present from the following dates, taken off Ven: August 1936; $^{12\text{-}13}/_{8}$-37 (common); $^{21}/_{8}$-37; $^{4}/_{9}$-37 (10 spms.); $^{12}/_{9}$-37; $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{23}/_{10}$-37; $^{17}/_{7}$-38 (30 spms.); $^{1}/_{8}$-38 (10 spms.); $^{3\text{-}9}/_{8}$-38 (common); $^{13}/_{8}$-38 (11 spms.); $^{26}/_{8}$-38; $^{11}/_{9}$-38; $^{4}/_{6}$-39; $^{17}/_{6}$-39; $^{3}/_{7}$-39 (85 spms.); $^{15}/_{6}$-39 (40 spms.); $^{5}/_{8}$-39; $^{18}/_{8}$-39 (15 spms.), and $^{16}/_{9}$-39.

In Helsingør plankton larvae are present from: $^7/_{10}$-41; $^{25}/_{10}$-41; $^{11}/_{11}$-41; $^{27}/_4$-42 (1 spm.); $^5/_5$-42 (1 young spm.); $^{20}/_6$-42 (1 very large spm.); $^6/_7$-42 (1 spm.); $^{18}/_7$-42 (4 young spms.); $^{17}/_8$-42 (34 in all stages, several of them very large), and $^5/_9$-42 (15 spms., mostly older larvae). From NE. Jutland (Frederikshavn) numerous larvae are recorded from plankton samples taken in July 1938. Thus the larva is common from early June to early November, with a maximum in July-August. Larvae in all stages of development from quite young to metamorphosing stages are equally common – a fact which shows that at least some of them are produced in the Sound or its nearest vicinity.

Aricidea suecica ELIASON. Rather common in the southern and middle parts of the Sound.

Reproduction: A. Literature. Nothing is known about the reproduction of this species. FEWKES (1883, pp. 174—176), however, describes and figures a couple of larvae which he refers to "*Aricidea sp.*(?)", but not the slightest information is given as to why he identifies the larvae as belonging to this genus. The larvae figured by FEWKES (pl. II, figs. 4—6, pl. VI, fig. 1) are so closely similar to young stages of Spionid larvae that they can hardly be distinguished from these larvae.

B. Own remarks. The identification of FEWKES mentioned above seems very dubious, and at least the larva of *Aricidea suecica* is totally unknown. In our plankton samples we have often seen larvae which bear a close resemblance to those referred by FEWKES to "*Aricidea sp.*(?)", but at present it seems impossible to solve this problem.

Paraonis lyra SOUTHERN. Three specimens known from a single find in the middle part of the Sound.

Reproduction: MCINTOSH (1923, monogr., p. 473) states that this species has "red ova". Nothing is known concerning the spawning time, the egg size, or the larval development. The reproduction is entirely unknown also in the Sound.

Paraonis gracilis TAUBER. Rather common in the northern and middle parts of the Sound.

Reproduction: Unknown in the literature. No observations from the Sound.

Paraonis fulgens LEVINSEN. Northern part of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Chaetopterus variopedatus (RENIER). Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. ENDERS (1909) has studied the reproduction of this species in North Carolina: It lives on sandy bottom. Sexual products spawned through the nephridia. Several thousand eggs spawned by a single female in 20 minutes. The larva hatches from the egg-membrane 5 hours after fertilisation and begins a pelagic life. The time necessary for a planktonic development varies considerably with the amount of food present. Young larvae in glass dishes swim near the surface, older larvae near the bottom. The young, tadpole-like larva (ENDERS, pl. II, figs. 9–10, MCINTOSH 1927, text figs. 28—29) has a terminal papilla, and eight days after fertilisation well nourished larvae will be able to adhere to a substratum by means of this papilla. Later on they will begin to swim again. The larva may take in animal food, i. a. Planarians and Copepods. ENDERS has observed and figured the metamorphosis. LO BIANCO (1899) records, from Naples, animals with mature sexual products in May to September, and pelagic larvae from January to February and from July, August, and September. McIntosh (1927) found larvae at St. Andrews in October and Flattely (1923, pl. V, fig. 15) off Northumberland in July. Allen (1915) records, from Plymouth, ripe eggs and sperms in July and larvae from July to October. Allen & Nelson (1911) have reared this species at Plymouth from the egg to the bottom stage, and according to Journ. Mar. Biol. Assoc. 1940, vol. 24, p. 692, Wilson is going to publish an account of the whole development.

B. Own remarks. The larva of *Chaetopterus variopedatus* was present in our samples from the Sound on two occasions only, viz. on $^{17}/_{9}$-41 between Hellebæk and Kulla Gunnarstorp, 30—0 m, 1 spm., and on $^{20}/_{10}$-41, plankton haul from the breakwater between Helsingor and Snekkersten, surface water, 1 spm. In the N.W. Kattegat (Frederikshavn) *Chaetopterus* larvae were very common in July 1939 at a depth of 5—6 m, and the figures given here are derived from this locality (fig. 56A—E). All larvae from the Sound as well as from Frederikshavn were about 900 to 1000 μ long and had 6 chaetigerous segments. The younger of them (fig. 56A—C) had only budding tentacles and one transverse ring of cilia round the body; the somewhat older larvae (fig. 56D—E) had distinct tentacles and two transverse rings of cilia round the body. The four eyes are of a carmine colour, two small carmine spots are seen on the "upper lip". The contents of the intestine are olive-green. Two lines of carmine pigment are seen on the sides of the anus, and the "tail" has a reddish-brown pigment at the tip.

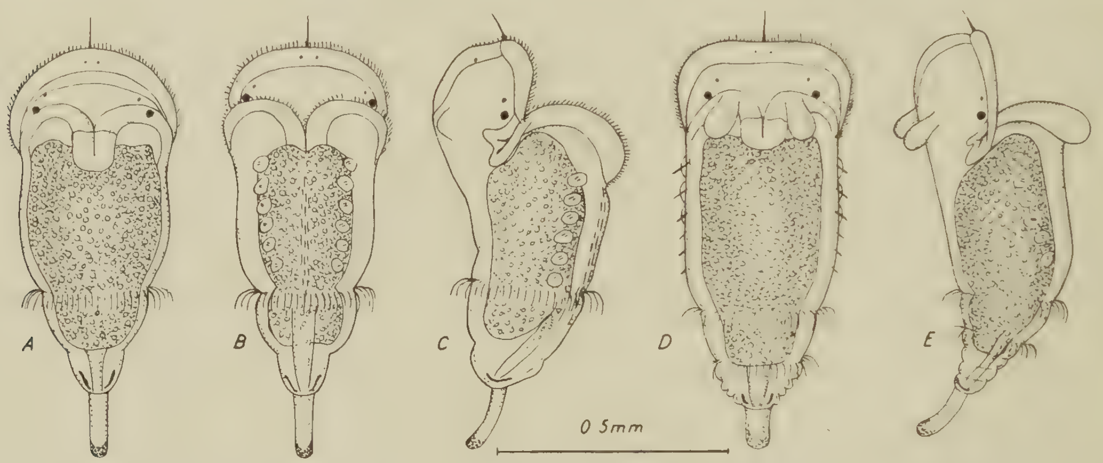


Fig. 56 A-E. *Chaetopterus variopedatus* (Renier). Larvae from plankton off Frederikshavn, NW. Kattegat, depth 5 to 6 m, caught and drawn from life on $^{28}/_{7}$-1939.—*A* to *C*. Younger larva with one ring of cilia only and with budding tentacles.—*A*. From the dorsal side, *B*. from the ventral side, C. from the right side.—*D* and *E*. Old larva with two ciliary rings and large tentacles. *D*. From the dorsal side, *E*. from the right side.

In bottle-collectors exposed at 16 m depth off Ven from $^{7}/_{7}$-39 to $^{24}/_{8}$-39 the just metamorphosed bottom stages of *Chaetopterus variopedatus* (about 2000 μ long, with 8 chaetigerous segments) were found in several specimens. Three weeks after metamorphosis these young animals had secreted thin, slimy tubes which adhered to the inner wall of the bottle-collectors, and each tube contained an animal like that seen in fig. 57A—B, which already showed several of the characteristics of the adults. The young animal is colourless; it has two large and two small black eyes. The foremost part of the intestine is olive-green, the hindmost part yellowish-brown. The oesophagus has a faint greenish pigment near the mouth, and a light olive-green bulbus just in front of the dark-green part of the intestine. — These finds seem to indicate that several larvae occur in the Sound. The fact that the larva is rare in our regular plankton series, seems to prove that the pelagic development takes place rather rapidly.

Spiochaetopterus typicus M. Sars. Northern part of the Sound (kind information from Dr. Eliason, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

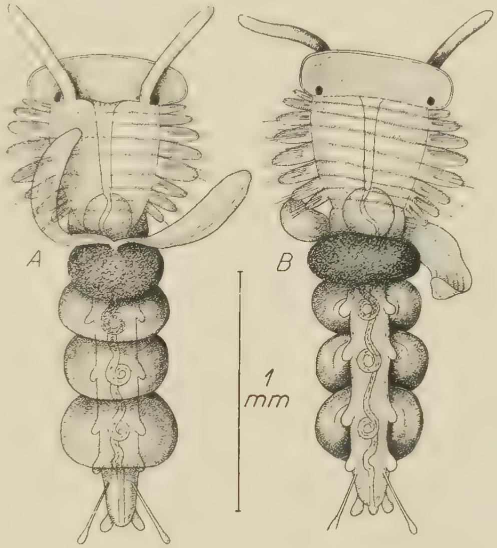


Fig. 57 A-B. *Chaetopterus variopedatus* (Renier). Young metamorphosed bottom stage, taken in a bottle-collector exposed off Ven at a depth of 16 m from $^{2}/_{7}$ to $^{24}/_{8}$-1939 (drawn from life on the latter date). The animals inhabited thin slime tubes, which adhered to the glass walls. — *A.* Seen from the dorsal and *B.* from the ventral side.

Cirratulus cirratus Müller. Middle and northern parts of the Sound, very common locally.

Reproduction: A. Literature. Cunningham & Ramage (1888, p. 646) have made the following observations on this species: Adult animals found under stones in March. The males were much smaller than the females, which were quite distended by eggs. Placed in aquaria they spawned their eggs, which were extruded one by one through a genital pore on either side of a great many segments. Immediately after spawning the eggs were imbedded in a slime secreted from the surface of the mother animal. These soft slime-masses of irregular shape and with the eggs inside adhered to stones and mud. McIntosh (1915, mgr., p. 252) says that "those from Guernsey and Herm in July and August had well developed ova". Fauvel (1916a, p. 448) mentions an observation on brood-protection in *Cirratulus cirratus* from the Falkland Islands. A large female had among its gills and tentacles a crowd of young larvae, 2 mm long, with twelve chaetigerous segments, two eyes, and with two pairs of tentacular cirri on the first segment (Fauvel figures this larva in pl. 8, fig. 12).

B. Own remarks. Nothing is known about the reproduction of this species in the Sound. The brood-protection mentioned by Fauvel (l. c.) seems to be of a very primitive kind, i. e. the slimy egg mass is kept between the tentacles and aërated there, instead of simply adhering to a substratum. There is nothing to indicate that the eggs and embryos near the Falklands are nourished by the mother animal. It seems most likely, therefore, that the unprotected egg mass of this species in boreal seas develops in precisely the same way as the protected egg masses near the Falklands. As, however, the embryos figured by Fauvel (l. c.) are 2 mm long and of a type very far from any pelagic stage, it seems likely that the species also reproduces without a pelagic stage in the Sound. As, furthermore, the adults are very common in the Sound, the larvae — if pelagic — must be frequent and very dominant in the plankton; but among the dominant or even the relatively frequent larvae in the plankton there was not a single form which could be referred with the slightest degree of probability to this species.

Chaetozone setosa Mgrn. Rather common in the middle and northern parts of the Sound.

Reproduction: A. Literature. McIntosh (1915, mgr., p. 266) writes about this species: "partially developed eggs occurred in the perivisceral cavity of an example captured in July.

In Norwegian examples large ova were present during the same month". Near Iceland Sæmundsson (1918, p. 205) observed a female with eggs in May. Day (1937) states that the eggs are sticky. Nothing is known about the egg size and the larval development.

B. Own remarks. Nothing is known about the reproduction in the Sound.

Cossura longicirrata Webster & Benedict. Southern and middle parts of the Sound, rather common.

Reproduction: Unknown in the literature. No observations from the Sound.

Dodecaceria concharum Ørsted. Boring in shells of *Cyprina* on the Hellebæk banks, depth 30 m. Living specimens found in 1941.

Reproduction: A. Literature. Mesnil & Caullery (1898a, 1898b) describe different forms of *Dodecaceria concharum* with different modes of reproduction: Form A: With 45—65 segments, one pair of palps, 4—6 pairs of gills, and no eyes. Sedentary. Only females occur. Reproduction atoquous, parthenogenetic, viviparous. Ripe, bluish-green ova, 160—200 μ across, develop in the body cavity to three-segmented larvae with a prostomium, two eyes, and yellowish-green pigment. A large number of larvae in the body cavity at the same time, whence they are later on "shed" through the nephridia. — Form B 1: Resembling A, but of a yellow colour and with other types of chaeta, and rudimentary gonads. These animals will later on metamorphose into Form B 2: an epitoquous form, with long bristles in the parapodia, two large eyes, atrophiated palps and reduced intestines. Males and females equally common. Yellow eggs, 200 μ across. — Form C 1: A later stage of form A, represented by very large specimens with yellow eggs. Only females are known. Develops later on into the epitoquous, but sedentary Form C 2: with palps, long parapodial bristles, two eyes, a reduced intestine, and yellowish eggs 120 to 140 μ across. Besides these sexual forms of reproduction at least two forms of asexual reproduction are commonly met with in this species (Martin 1933, Dehorne 1924, 1927).

B. Own remarks. The single adult specimen found in the summer of 1941 (on $^{26}/_{7}$; 25—33 m, in an old shell of *Cyprina*) off Hellebæk showed all the characteristics of form A, but seemed not to be in the season of reproduction. According to the literature cited above, this form may be expected to be parthenogenetic and viviparous, but nothing has been ascertained as to these features in the Sound.

(Streblospio shrubsolii (Buchanan) cf. p. 95).

Stylarioides (Trophonia) plumosa Müller. Common in the northern and middle parts of the Sound.

Reproduction: McIntosh (1915, mgr., p. 94) cites various observers, who state that the ova are of a grassy-green colour. My experiences from *Stylarioides glaucus* seem to indicate that the ova are green when preserved in alcohol, but yellow in a living state. — Reproduction unknown from the Sound.

Stylarioides (Diplocirrus) glaucus Mgrn. Northern part of the Sound, rather rare.

Reproduction: A. Literature. Large ova in July near Scotland (McIntosh 1915, mgr., p. 98).

B. Own remarks. A female taken off Hellebæk, 25—33 m, on $^{26}/_{7}$-41, contained large numbers of ova. When stirred, the animal "spawned" a lump of eggs through a rupture in the body wall. These eggs (fig. 58), of a deep yellow colour (green in alcohol), seemed to be quite ripe. They were all of precisely the same size (140 μ across) with a distinct zona pellucida (10 μ thick), they were rich in yolk, and quite opaque. Nothing is known about the larval development, which according to the egg type and to our experience as regards planktonic larvae in the Sound must be presumed to be non-pelagic.

Flabelligera affinis M. Sars. Rather common in the northern and middle parts of the Sound.

Reproduction: A. Literature. In June, July, and August brownish or greenish-brown, apparently mature ova of this species have been observed by different authors (McIntosh 1915, mgr., p. 112). Mature females had the body cavity crowded with ova showing through the body wall. The sperm is white, and the colour indicates the sex of the mature examples. The antarctic species *Flabelligera mundata* has brood-protection between its gills (Gravier 1923, p. 193).

B. Own remarks. *F. affinis* is very common in high-arctic regions, thus for instance in the East Greenlandic fjords, but regular plankton hauls made during the whole year in these fjords yielded no larvae which could be referred to this species. As, further, high-arctic invertebrates show a tendency to reproduce without any pelagic stage, it seems probable that this mode of reproduction is also the rule in *Flabelligera affinis*. Nothing is known concerning the reproduction in the Sound.

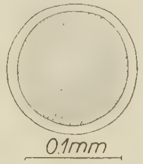


Fig. 58. *Stylarioides (Diplocirrus) glaucus* Mgrn. Ripe egg taken from a female captured off Hellebæk at 25—33 m depth, on $^{26}/_{7}$-1941. The female in question "spawned" when stirred several eggs (drawn from life on $^{26}/_{7}$-1941).

Brada villosa Rathke. Northern and middle parts of the Sound, common.

Reproduction: A. Literature. Unknown.

B. Own remarks. Nothing is known from the Sound, but this species, also, is very common in high-arctic seas and its larvae therefore probably develop without any pelagic stage.

Scalibregma inflatum Rathke. Northern part of the Sound, rare.

Reproduction: A. Literature. Fage & Legendre (1925) observed the swarming of adult ripe animals at the surface off Concarneau in October to December. The swarming animals were partly epitoquous and spawned their sexual products through ruptures in the body wall.

B. Own remarks. A bottle-collector exposed off Ven at a depth of 16 m from $^{24}/_{7}$—$^{12}/_{8}$-40 contained two young animals, $4^{1}/_{4}$ and $5^{1}/_{2}$ mm long respectively, which had settled in the collectors within the period mentioned. As the collector was placed 2 m above the sea-bottom, this seems to show that the larvae are able to swim or float in the water — at least for a few hours. A truly pelagic stage hardly occurs in this species, but nothing definite is known so far.

Eumenia crassa Ørsted. Middle and northern parts of the Sound. Very common on soft bottom at depths of 30—40 m.

Reproduction: Nothing is known concerning the reproduction in the Sound. Masses of pink eggs floating freely in the body cavity were observed in a female in July 1942 off Helsingor. Dr. H. BLEGVAD has kindly informed me that adults of this species taken north of Ven in stomachs of cod on $^{27}/_{9}$-25 were filled with numerous large ova. Hence it seems most probable that the breeding season is in the autumn; this is in good agreement with the spawning of other animals at the depths at which this species has its main occurrence. Nothing is stated in the literature concerning its reproduction.

Ophelia limacina RATHKE. Northern part of the Sound, very common locally on hard sandy bottom.

Reproduction: A. Literature. Nothing is known about the reproduction of this species. — MCGUIRE (1935) and BROWN (1938), however, have published the following observations on the closely related *Ophelia cluthensis* from Scotland: Breeding in April and September. The sexual products are probably shed through local ruptures of the body wall. The ripe eggs are white discs, their flattened surface being almost circular in outline. They are about 140—150 μ in diameter and about 50—60 μ thick (egg membrane only 5 μ thick). Larval stages older than the four-cell stages are as yet unknown. Eggs fertilised in April will probably develop into young worms, 2 mm in length, in June of the same year.

B. Own remarks. Females of *Ophelia limacina* taken at a depth of 10 m off Hellebæk on $^{10}/_{4}$-42 contained large numbers of apparently ripe ova of precisely the same shape as stated above for *O. cluthensis*. The size of the eggs, however, was not noticed.

Ammotrypane aulogaster RATHKE. Common in the northern part of the Sound.

Reproduction: Unknown in the literature. No observations from the Sound.

Travisia forbesi JOHNSTON. Northern part of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Arenicola marina LINNÉ. Very common throughout the Sound.

Reproduction: A. Literature. BLEGVAD (1923) observed the shedding of eggs and the early larval stages of this species near Nyborg on $^{6}/_{8}$-22. A thin, reddish-yellowish layer of eggs was deposited on the surface of the sand within a circle of about 20 cm in diameter around the habitat of the mother animal. The eggs are stirred by the slightest movement of the water and under natural conditions they will undoubtedly spread in the water masses immediately after having been spawned. The egg is discoidal, longest diameter 130 μ. The first larvae hatch four days after fertilisation; they are telotrochous, 200 μ long, with two brownish eyes, long sensual hairs in front, of a yellowish-white colour, and swim briskly about. Two days later the first setae appear, and 7 days after hatching the larvae, now 250 μ long, have three chaetigerous segments and two pairs of eyes. BLEGVAD (l. c.) gives good figures of the larvae, which died at this stage of development, but he has seen larvae with 5 chaetigerous segments in nature in September. — PIRLOT (1933) has observed spawning along the Belgian coast, and states, on the basis of observations in three different years, viz. 1928, 1932 and 1933, that the whole spawning was completed within two days, viz. on $^{13\text{-}14}/_{10}$, $^{14\text{-}15}/_{10}$, and $^{6\text{-}7}/_{10}$ respectively in the 3 years mentioned. These observations seem to show that the parent animal spawns *in situ*, not swimming at the surface. STORROW (1925) observed spawning *Arenicola marina* on $^{23\text{-}24}/_{9}$-24 on Cullercoates Sands. CUNNINGHAM & RAMAGE (1888) mention spawning in August —September in the Firth of Forth. ASHWORTH (1904) states, from British waters, that ripe sexual products were found in two periods a year, viz. February to April and July to October, but he has never seen spawning animals. Orton (1933a) found large numbers of nearly ripe males and females at Cheshire on July 19th. Allen (1915) mentions the occurrence of post-larvae of *Arenicola* in tow-nettings in February and March. Blegvad (l. c.) sets forth the hypothesis that the species breeds in the autumn and "that the duration of the pelagic life of the larvae is very considerable, extending, perhaps, over the whole winter", but he adds that this problem still remains unsolved. Thamdrup (1935) states that the spawning at Skallingen takes place in the late summer and autumn. He mentions, further, that the smallest bottom stages of this species are not found in the autumn, winter, and spring, but in the summer — a fact which seems to support the hypothesis that the species has a long pelagic life. Ashworth (1904) and Blegvad (1923) record the so-called "Benham-stage" of this species from plankton taken in March to June, i. e. post-larvae, 3.9 to 6.5 mm long, with three distinct sections of the body developed, but still without gills. They were found floating in the plankton, and were surrounded by a gelatinous tube secreted by themselves.

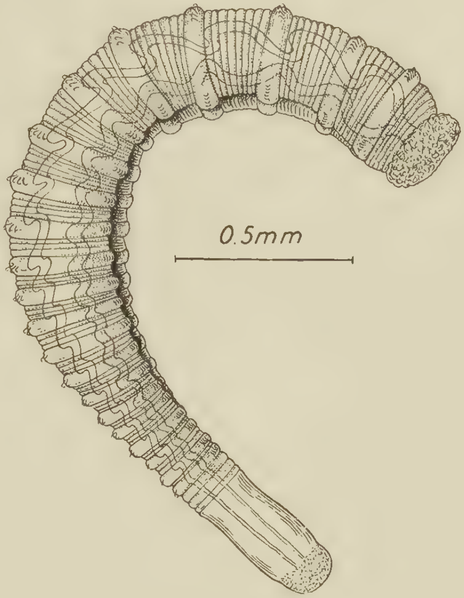


Fig. 59. *Arenicola marina* Linné. Young bottom-stage dissected out of its slime tube (see the text p. 110). From a bottle-collector exposed off Ven, at a depth of 16 m, from $^{24}/_{7}$ to $^{13}/_{8}$-1940 (drawn from life on $^{14}/_{8}$-1940).

B. Own remarks. Adult specimens from Julebæk, N. of Helsingør, were unripe in the spring; in August sexual products had begun to develop, but were still far from ripe. There can hardly be any doubt that the main spawning takes place in the autumn, as stated by most of the authors cited above. As stated above, the adult *Arenicola marina* is very common in the Sound, where it is found in very large specimens. Knowing the larval type described by Blegvad (l. c.), we looked very zealously and carefully for such larvae in our regular plankton hauls taken during three years at Ven and one year at Helsingør. Several plankton hauls from Ven taken across the *Zostera*-meadows were likewise examined. However, not a single larva was found in our samples. The frequency of the mother animals in the Sound and the total absence of the larvae in the "high-sea plankton" of the Sound seem to show that the pelagic stage — if any — is very short, in contrast to the hypothesis of Blegvad and Thamdrup. The larval type (Blegvad, p. 2, figs. e—h) bears a fairly close resemblance to the larvae of *Scoloplos armiger* figured by Grooth (1907, fig. 9 A, B), the latter being more ciliated, i. e. more fit for a pelagic life than that of *Arenicola marina*. The larvae of *Scoloplos armiger* are, however, non-pelagic and there is every indication that the larvae of *Arenicola marina* belong to the type that develops with a very shortened pelagic stage, if it has a pelagic stage at all.

In the autumn of 1943 Erik Smidt found the young, just hatched larvae of *Arenicola marina* crawling among the sand grains in the tidal zone at Esbjerg. In spite of the adults being dominants of the tidal zone proper, only very few larvae were obtained in regular plankton hauls during two years. This provides the final proof of the non-pelagic or shortened pelagic development of these larvae. A detailed account of the observations will be published later by E. Smidt, who, however, has kindly allowed me to mention his results. —Dr. G. Gustafson, leader of the Swedish Zoological Station Kristineberg, has kindly allowed me to mention his observation, that the development is non-pelagic also in the Gullmarfjord.

The facts recorded from other areas, viz. that the young bottom animals are first met with in the summer, may be explained by assuming that the young larvae settle in the autumn soon after they have been hatched; then follows a stagnation in the growth of these tiny bottom stages during the whole winter, until the rise of the temperature in the spring (which is especially strongly felt in the shallow-watered areas in which *Arenicola* lives) will suddenly cause the growth to start afresh. Such a rhytm was ascertained in the Sound for instance in *Mytilus edulis* — an inhabitant of the same areas and the same depths. The "Benham-stages", known from British waters and from Nyborg in Denmark in the spring, have never been observed in the Sound; this could hardly have been avoided, if they were present here in large numbers. Dr. Blegvad has kindly placed his fixed material of "Benham-larvae" i. a. from Nyborg at my disposal. Their identity with *Arenicola* seems unquestionable. — The present author, however, has never seen such larvae in the Sound.

In a bottle-collector exposed off Ven at a depth of 16 m from $^{24}/_{7}$ to $^{13}/_{8}$-40 a single young bottom stage in a slimy tube was found to adhere to the glass-wall (fig. 59). This young animal, which in my opinion should be referred to *Arenicola marina*, was 2.8 mm long, i. e. 1 mm smaller than the smallest "Benham-stages" known (3.9 mm), and the three sections of the body had not yet differentiated. In spite of its tiny size this young stage was sedentary. — As my experience is limited to the material from the Sound recorded here, I am unable to explain the occurrence of pelagic "Benham-stages" in other sea-areas. Probably the "Benham-stages" are not pelagic in the common sense of the word, but are specimens metamorphosed in "mid-water" or young bottom-stages, which with their slime tubes have been stirred up by movements of the water; these will easily stir the bottom in the shallow-watered areas in which the animals live. Meek & Storrow (1924) have shown that also adult specimens of *Arenicola* are able to float in the water in similar slime tubes as are known for the Benham-stage. It is, however, not quite impossible that the larval development varies, having a longer or a shorter pelagic stage from place to place. Thus it is known that near Japan the closely related species *Arenicola claparedii* has a pelagic stage (Okuda 1938), while in Puget Sound it has a non-pelagic development (Guberlet 1934). See, however, the discussion on p. 467.

Capitella capitata Fabr. Northern and middle parts of the Sound, common.

Reproduction: A. Literature. Eisig (1887, pp. 280—287 and 791—793; 1899) describes at length the reproduction as well as the larval stages in this species from Naples. His observations may be summarised as follows: The males and females have copulatory organs. The males will copulate with ripe as well as unripe females, unripe males, and juvenile specimens. The sperms are transferred to the female in spermatophores, and will keep alive in unripe females until the eggs are ready to be fertilised. Ripe animals occur at Naples from November to May with a maximum in January-February. The fertilised female spawns its eggs in its tube, where the female will remain, protecting the brood until the larvae hatch. In the summer 10—12 days and in the winter 12—14 days will elapse from the fertilisation of the egg to the hatching of the larva. The hatching larva has 13 segments, all with chaeta, it is telotrochous, positively phototactic, and swims briskly about. Four or five days after hatching the ciliary rings will diminish, and seven days after hatching the larva will sink to the bottom and bury itself in the sand. The number of segments in the young bottom-stage is the same (13) as in the hatching larva, but soon after settling a rapid growth will take place. Claparède

& Metschnikoff (1869) and Leschke (1903) give good figures of the larvae and add the following particulars to the description of Eisig: The telotrochous larva has two red eyes in its older stages, the ventral side is provided with cilia, fine greenish pigment is seen in the furrows between the segments and over the whole anal segment. The three first segents have bristles, the following segments bear hooks. Mouth and intestine are well developed. Hofker (1930, pp. 198—199) describes and figures larvae of a Capitellid from the Zuidersee, which he refers without doubt to *Capitella capitata.* They are 380 μ long, with 6—7 chaetigerous segments, telotrochous, with two eyes behind (!) the prototroch. Greenish pigmentation. Day (1937) states that the larva of *Capitella capitata* "was not seen to contain food till after metamorphosis". He further figures and describes the non-pelagic larvae of *Capitellides giardi,* and summarises the characteristics of Capitellid larvae as a whole.—Finally, Aiyar (1933) describes larvae of an unknown species of *Capitella* from the Madras harbour (India).

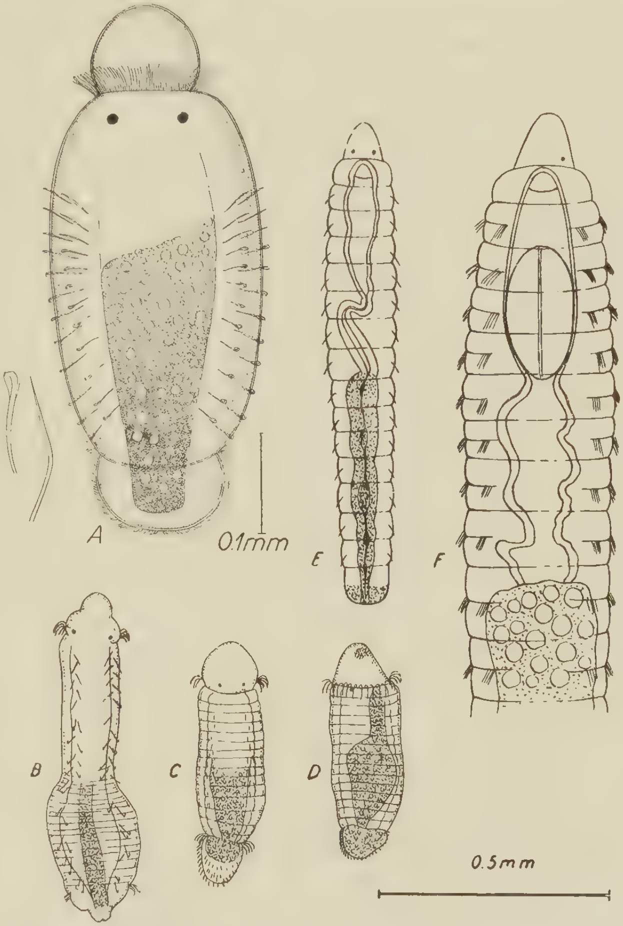


Fig. 60 A-F. *Capitella capitata* Fabr.—*A.* Old larva seen from the dorsal side. From plankton off Ven, depth 18 to 0 m, taken on $^{26}/_{8}$-1944 (drawn from life the same day). Bristles from segment I and segment XII are figured in larger magnification.—*B* to *D.* Rough sketches of planktonic larvae from the same depth and locality to show the variation in shape when they swim in the water (caught and drawn from life on $^{5}/_{1}$-1938). *B* and *C.* From the dorsal side, *D.* from the right side.—*E.* Just metamorphosed bottom stage from a bottle-collector exposed off Ven, depth 16 m, from $^{24}/_{7}$ to $^{12}/_{8}$-1940 (drawn from life on $^{13}/_{8}$-1940).—*F.* Front part of older bottom-stage from the same bottle-collector and the same date (drawn from life on $^{13}/_{8}$-1940).

B. Own remarks. Larvae of this type (fig. 60 A—D) have been taken in our plankton hauls off Ven on: $^{18}/_{12}$-37 (8 spms.); $^{5}/_{1}$-38 (5 spms.); $^{3}/_{4}$-38 (5 spms.); $^{26}/_{8}$-38 (3 spms.); $^{25}/_{9}$-38 (1 spm.); $^{12}/_{11}$-38 (5 spms.); $^{22}/_{12}$-38 (1 spm.); $^{25}/_{3}$-39 (10 spms.); $^{10}/_{4}$-39 (1 spm.); $^{30}/_{4}$-39 (2 spms.); $^{17}/_{5}$-39 (4 spms.); $^{4}/_{6}$-39 (6 spms.); $^{17}/_{6}$-39 (1 spm.); $^{3}/_{7}$-39 (10 spms.); $^{15}/_{7}$-39 (2 spms.); $^{5}/_{8}$-39 (3 spms.); $^{16}/_{9}$-39 (1 spm.), and off Helsingør on: $^{7}/_{10}$-41 (1 spm.); $^{2}/_{12}$-41 (3 spms.); $^{21}/_{2}$-42 (6 spms.); $^{21}/_{3}$-42 (3 spms.); $^{27}/_{4}$-42 (3 spms.); $^{15}/_{5}$-42 (3 spms.); $^{20}/_{6}$-42 (1 spm.); $^{18}/_{7}$-42 (2 spms.), and $^{17}/_{8}$-42 (1 spm.). Larvae have thus been found in all the months of the year. This fact may probably be accounted for by the occurrence of the adult animals in shallow as well as in deeper water, where the temperature maxima are found at quite different times of the year. The larva agrees in all essentials with those figured by Claparède & Metschnikoff (1869) and Leschke (1903), those from the Sound, however, having 12 chaetigerous segments (not 13 as at Naples). The colour of the intestine may vary from greyish, greyish-brown, and olive-green to verdigris and navy-blue.

A bottle-collector exposed off Ven at a depth of 16 m from $^{24}/_{7}$—$^{12}/_{8}$-40 contained a just metamorphosed bottom-stage somewhat more than 1 mm long, with 17 chaetigerous segments (fig. 60 E). The first three chaetigerous segments had only normal capillary bristles, the following segments were all provided with hooks. The hindmost part of the intestine was navy-blue to ærugo-green, and contained detritus of a greyish-green colour. The anal-segment had navy-blue pigment. The eyes were red. The same bottle-collector contained a *Capitella capitata*, 2 cm long, and as the collector was placed 2 m over the bottom, the specimen must be supposed to have developed from the larval stage in the course of 20 days. This supposition is in good agreement with the observations of Claparède & Metschnikoff (l. c.), viz. that a rapid growth will take place after the larva has settled. These tendencies are supported by further observations from 1940. Another bottle-collector exposed off Ven at 16 m depth from $^{24}/_{7}$—$^{12}/_{8}$ contained three young bottom-stages of *Capitella capitata* of a length of 2 mm (cf. fig. 60 F), $3^{1}/_{2}$ mm, and $6^{1}/_{2}$ mm respectively. They were all embedded in slime-tubes secreted by themselves and had grown from larvae to their present size in the course of only 20 days.

Thus, in the Sound, *Capitella capitata* seems to spawn all the year round and to grow very rapidly after settling.

Notomastus latericeus Sars. Northern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. McIntosh (1915, mgr., p. 279) states that the ova are red or brownish-red, and that the sperm is whitish. Wilson (1933) has reared, described, and figured the larva. His results are briefly as follows: Ripe specimens were slit open, artificial fertilisation was undertaken; the fertilised eggs were washed free from sperms, and developed normally. A ripe egg is 150 μ across. The larvae swim by means of a prototroch 15 hours after fertilisation, and the egg membrane forms part of the larval cuticle. A larva 24 hours old is in the *Trochosphaera*-stage. The following larval stages have reddish-brown eyes, and their shape is very similar to that of the *Capitella*-larva. The contents of the intestine are yellowish-green. While, however, the *Capitella*-larva has 12—13 chaetigerous segments during the whole pelagic life, the *Notomastus*-larva will already leave the plankton when 5 chaetigerous segments have developed, i. e. when it is 10 days old and about 380 μ long. Further, the prototroch of the *Notomastus*-larva is broader than that of the *Capitella*-larva. The *Notomastus*-larva will not take any food till after metamorphosis (Wilson 1937).

B. Own remarks. While the intestines of the larvae of *Capitella capitata* are often of an intense navy-blue to ærugo-green colour, the intestines of *Notomastus*-larvae are yellowish-green. Such Capitellid-larvae with a greenish intestine and differing in appearance from those of *Capitella* were found in the Helsingor plankton on: $^{2}/_{12}$-41 (3 larvae), $^{21}/_{2}$-42 (3 larvae), and $^{27}/_{4}$-42 (3 larvae). It seems most reasonable to refer these larvae to *Notomastus latericeus*, but unfortunately the number of chaetigerous segments of these larvae were not examined, so the definite proof cannot, therefore, be given. It is quite possible that in the years 1937—1938 larvae of this species were referred to *Capitella capitata*, as our knowledge of these larvae has been considerably increased during our study of them. Two bottle-collectors exposed off Ven at 16 m depth from $^{5}/_{7}$ and $^{7}/_{7}$-39 respectively to $^{2}/_{9}$-39 contained a few young bottom-stages of *Notomastus*, 10—20 mm long. A bottle-collector exposed at the same depth and in the same locality from $^{17}/_{9}$—$^{21}/_{10}$-39 contained 10 specimens of *Notomastus*, likewise 10—20 mm long. This seems to show that *Notomastus*, like *Capitella*, grows very rapidly as soon as settling has taken place.

Heteromastus filiformis (Claparède). Northern part of the Sound; rather common (kind information from Dr. Eliason, Göteborg).

Reproduction: Unknown in the literature. No observations from the Sound.

General Remarks on the Reproduction in *Maldanidae.*

It is surprising that a rather large and very characteristic family like the *Maldanidae* is almost entirely unknown as regards reproduction and larval development. A study of the copious literature used for the present paper has only supplied me with the following facts: Wilson (1882) mentions, from North Carolina, a species of *Clymenella* – probably *Clymenella* (*Axiothea*) *mucosa* — which deposits its eggs in a jelly-mass of the size and shape of a pigeon's egg. This egg-mass is fastened to the mouth of the tube. Mead (1897) mentions the spawning of *Clymenella torquata* near Woods Hole; it spawns within a period of only two or three days in April or May. The very yolky eggs, 150 μ across, are spawned singly, being shed freely in the water in the night, and are at once widely distributed by the movements of the water. Finally, observations in the Sound seem to show that *Nicomache lumbricalis* has very large eggs (500 μ across) very rich in yolk. The size as well as the type of this egg seem to show that the larval development is non-pelagic (cf. the remarks on *Nicomache lumbricalis* below). In the earlier literature (cf. Claus-Grobbens' Lehrbuch 1928) the *Mitraria*-larvae are stated to belong to the family *Maldanidae,* but fresh investigations (e. g. Wilson 1932 b) have shown that only the family *Oweniidae,* not the *Maldanidae,* produce larvae of the *Mitraria* type. The larval stage of the *Maldanidae* is, therefore, still less known than it was supposed to be a few years ago! — All seems, however, to point to a non-pelagic development in this family. The very yolky eggs of *Clymenella torquata,* the extraordinarily large eggs of *Nicomache lumbricalis,* and the fact that the plankton from the Sound contains no larvae which can be referred even with the slightest probability to the *Maldanidae,* are the criteria on which this conception is based.

Praxillura sp. One fragment of an unknown species of this genus is known from the northern part of the Sound.

Reproduction: Unknown in the literature for the whole genus. Nothing known from the Sound.

Rhodine gracilior Tauber. Northern and middle parts of the Sound, extremely common locally.

Reproduction: Unknown in the literature for the whole genus. Nothing known from the Sound.

Nicomache lumbricalis var. borealis Arwidsson. Middle and northern parts of the Sound, common.

Reproduction: A. Literature. Unknown.

B. Own remarks. A large female captured off Hellebæk, 25—33 m depth, on $^{26}/_{7}$-41, contained a number of white eggs. Some of them were still rhomboid and densely crowded, but the greater part of them were free, apparently ripe, and all of the same size. The yolky eggs (fig. 61) were 500 μ across, the vitelline membrane

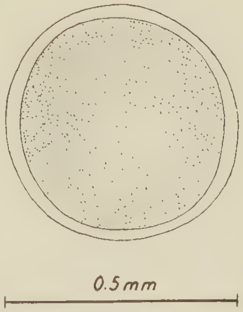


Fig. 61. *Nicomache lumbricalis* Arwidsson. Ripe egg from a female captured off Hellebæk, depth 25 to 33 m, on $^{26}/_{7}$-1941 (drawn from life the same day).

was 25 μ thick. Eggs of this size, according to the experience gained so far, will develop in a non-pelagic way.

Nicomache trispinata Arwidsson. Found on two occasions in the middle and northern parts of the Sound.

Reproduction: Unknown in the literature. No observations from the Sound.

Petaloproctus tenuis var. borealis Arwidsson. Middle and northern parts of the Sound, common locally (Hellebæk).

Reproduction: Unknown in the literature. No observations from the Sound.

Praxilella prætermissa Mgrn. Northern and middle parts of the Sound, very common.

Reproduction: Unknown in the literature. No observations from the Sound.

Euclymene droebachiensis G. O. Sars. Middle and northern parts of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Maldane sarsi Mgrn. Northern and middle parts of the Sound, common in the northern part.

Reproduction: Unknown in the literature. No observations from the Sound.

Owenia fusiformis Delle Chiaje. Northern part of the Sound, not very common.

Reproduction: A. Literature. McIntosh (1915, mgr., p. 362), mainly on the basis of Watson's observations (1901), states about this species: "In May both male and female elements are discharged by two pores to the right and left of the vent — a portion of the posterior end of the body in the males projecting from the anterior aperture of the tube. The ova are enveloped in a gelatinous mass placed near the tube". The eggs are yellow. The spawning time is May to June. Watson (1901), McIntosh (1927), and especially Wilson in his very beautiful paper (1932b) give figures of the larvae in all stages of development. Wilson's results are as follows: Ripe adult specimens occur near the British Isles from March to July. Main spawning (in June) very short. Artificial fertilisation. Eggs 100 μ across, with an egg membrane 1 to 2 μ thick. Swimming larvae two days after fertilisation. The typical *Mitraria*-stage (the *Trochosphaera*) is formed two or three days after fertilisation, and the larvae will not leave the plankton and metamorphose until four weeks after fertilisation. The late larva has a maximum diameter of the umbrella of 500 μ, and a length from the chaeta-sacs to the head of 300 μ. A 6-lobed, large, open umbrella; the base of the metatroch is colourless or faintly cream-coloured. The metamorphosis has a "catastrophic" character just as the metamorphosis of *Polygordius* described by Woltereck.

B. Own remarks. *Mitraria* larvae are common in the Sound in the spring and early summer, but they are very small and do not belong to *Owenia* but to *Myriochele danielsseni* (see below). Only once, on $^3/_7$-39, a single *Mitraria* larva occurred in our samples, which according to its large size and its open, lobed umbrella showed all the characteristics of the *Owenia* larva. As the *Mitraria* larvae in our samples were always examined very carefully, it can be taken for granted that the *Owenia* larvae play a rather insignificant part in the plankton of the Sound.

Myriochele danielsseni Hansen. Northern and middle parts of the Sound, exceedingly common locally in deep water.

Reproduction: A. Literature. The reproduction of this species is quite unknown. Wilson (1932 b, pp. 234 and 322—324, text figure 50) figures a larva found by himself in the Firth of Clyde, and writes: "I think it likely that it will prove to be the larva of *Myriochele*, possibly *M. Heeri* Malm. . . ." (a species closely related to *M. danielsseni*) This larva, which is very common in the Firth of Clyde in September to December with a maximum in October, according to the figures and text of Wilson differs from the larva of *Owenia fusiformis* on the following points: Very small (maximum diameter 240 μ; length from the chaeta-sacs to the head 180 μ), umbrella bell-shaped, very faintly lobulated along the margin; two types of chaetae, viz. normal capillary rods and club-shaped bristles. Wilson states that this *Mitraria* belongs to the *Oweniidae*, but his reference of it to *Myriochele* is merely based on a supposition.

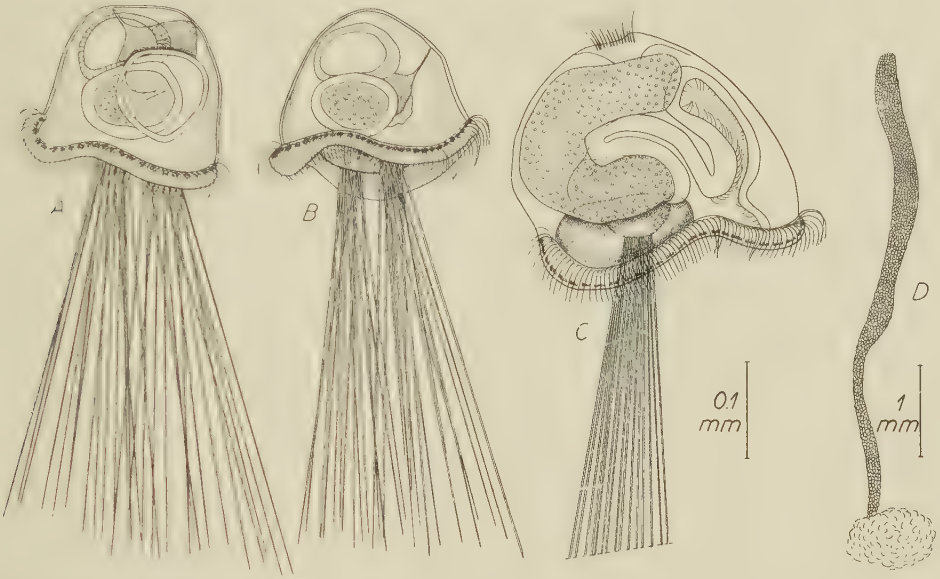


Fig. 62 A-D. *Myriochele danielsseni* Hansen. Larvae from plankton, drawn from life. — *A* and *B*. Larvae of the size normally met with in large numbers. Off Ven, depth 18 to 0 m, taken on $^{25}/_{3}$-1939 (drawn on $^{26}/_{3}$-39). — *C*. Older larva presumably belonging to the same species (see the text p. 116). Between Hellebæk and Kulla Gunnarstorp, depth 35 to 0 m, caught and drawn on $^{15}/_{5}$-1942. — *D*. Tube of a just metamorphosed bottom stage of *Myriochele danielsseni* from a bottle-collector exposed off Ven, depth 16 m, from $^{27}/_{5}$ to $^{17}/_{7}$-1941 (drawn with the living animal inside on $^{18}/_{7}$-1941). The 0.1 mm scale refers to figs. A, B and C.

B. Own remarks. In the spring and early summer *Mitraria*-larvae were met with in fairly large numbers in plankton hauls from the Sound. Apart from the larval *Owenia* mentioned above, they all seem to belong to one and the same species, and agree on several points with the larvae which were referred by Wilson (l. c.) to *Myriochele heeri*. Since, however, *Myriochele danielsseni* is the only Oweniid besides *Owenia fusiformis* which is recorded from the Sound, where it is common, as are also the *Mitraria* larvae in question, it seems justifiable to refer the larvae to this species. Such larvae are present in our plankton-series taken off Ven on: $^{23}/_{5}$-37 (10 spms.); $^{6}/_{6}$-37 (50 spms.); $^{21}/_{6}$-37 (3 spms.); $^{3}/_{4}$-38 (5 spms.); $^{18}/_{4}$-38 (14 spms.); $^{10}/_{5}$-38 (11 spms.); $^{25}/_{3}$-39 (5 spms.); $^{10}/_{4}$-39 (2 spms.), and $^{17}/_{5}$-39 (2 spms.), and off Helsingør on: $^{10}/_{4}$-42 (2 spms.), and $^{27}/_{4}$-42 (2 spms.); thus they occur in the Sound plankton from April to June. The larvae from the Sound (fig. 62 A-B) have a maximum diameter of 200 to 220 μ and a length from the chaeta-sacs to the head of 160 μ, i. e. measurements agreeing fairly well with those of the larva of *M. heeri*. The umbrella is bell-shaped, the lobulation is very faint, and the base of the metatroch has pink spots of pigment. Only capillary bristles were, however, seen among the chaeta. The prototroch was not seen, but has probably been contracted when the animals were placed under the microscope.

As mentioned above, larvae of this type were common in plankton from April to June, and accordingly young metamorphosed bottom-stages were to be expected already in May and June. Bottle-collectors exposed off Ven at a depth of 16 m from $^{27}/_{5}$ to $^{17}/_{7}$-41 contained 120 young bottom-stages of Polychaetes (fig. 62 D) in thin tubes of clay, $2^{1}/_{2}$ to 3 mm long. Owing to the numerous uncini on each segment and their characteristic heads these young worms were easily identified as *Myriochele danielsseni* – a fact which seems to confirm the identification of the larva given above.

A main series taken off Helsingor on $^{11}/_{11}$-41 contained a young bottom-stage of *Myriochele* in a 12 mm long tube. This specimen had probably been whirled up in the water by the extremely strong current on that particular day. As the last planktonic larvae were observed in the Sound in June, it seems likely that the bottom-stage in question was at least five months old.

Off Helsingør *Mitraria*-larvae occurred in the main series from $^{15}/_{5}$-42 (11 spms.) and $^{20}/_{6}$-42 (1 spm.), which in colour and shape closely resembled the larvae here referred to *Myriochele danielsseni* (see above), but were of a much larger size (fig. 62C). The umbrella measured about 300 μ across and had a length from the chaeta-sacs to the head of 225 μ. The umbrella was faintly four-lobed, bell-shaped as in the *Myriochele*-larvae, and the base of the metatroch was yellowish-pink in colour. The prototroch is distinct. The larvae in question seem accordingly to agree much more closely with the small larvae of *Myriochele* described above than with the larva of *Owenia fusiformis* (which see), and it seems most reasonable to regard them as older stages of *Myriochele danielsseni*. If I am right in this assumption, the larvae of *M. danielsseni* attain a somewhat larger size before leaving the plankton than those belonging to *M. heeri* and described by Wilson (see above).

Pectinaria auricoma Müller. Middle and northern parts of the Sound, common.

Reproduction: A. Literature. Nilsson (1925) states from Kristineberg that the growth of adult specimens is very slow, and that the individual specimens live for more than one year. He found ripe animals as late as August and September which had not yet spawned. McGinitie (1935, p. 695), who studied this species at California, found that it "spawns in the spring. Eggs and sperm are given off from the tip of the last segment of the animal. When spawning this tip elongates and the eggs or sperm issue in a stream". Sømme (1927) has described and figured larvae of *Pectinaria* from Lenefjord in Norway which to all appearance may be referred to *Pectinaria auricoma*. Criteria for this supposition are: The water masses of Lenefjord are nearly entirely separated from the open sea; and the larvae occurred in Lenefjord in rather large numbers. Bottom-samples showed that *Pectinaria auricoma* and *P. koreni*, and only these two species, were common in the fjord. The tubes of the larvae showed the same proportion between length and diameter as those of the adult *Pectinaria auricoma*, while the larval tubes of *P. koreni*, described and figured by Nilsson (1925), are proportionately much wider; this is also in good agreement with the proportions of the tube in the adult *P. koreni*. The length of the larval tubes which are referred by Sømme (l. c.) to *P. auricoma*, is 3.0 to 3.4 mm, the largest diameter 0.35 to 0.37 mm. The larvae which inhabited these tubes were 1.3 to 1.5 mm long, i. e. less than half the length of the tube. The thin tubes consist of a hardened slime of a structure as if they were joined together of rhomboid plates. — Hofker (1920—1922, p. CLXII) mentions from plankton taken off den Helder (Holland) in May numerous Metatrochophores of "*Pectinaria auricoma* (= *belgica*)". From his description (no figures) it seems impossible to decide to which species his larvae belonged.

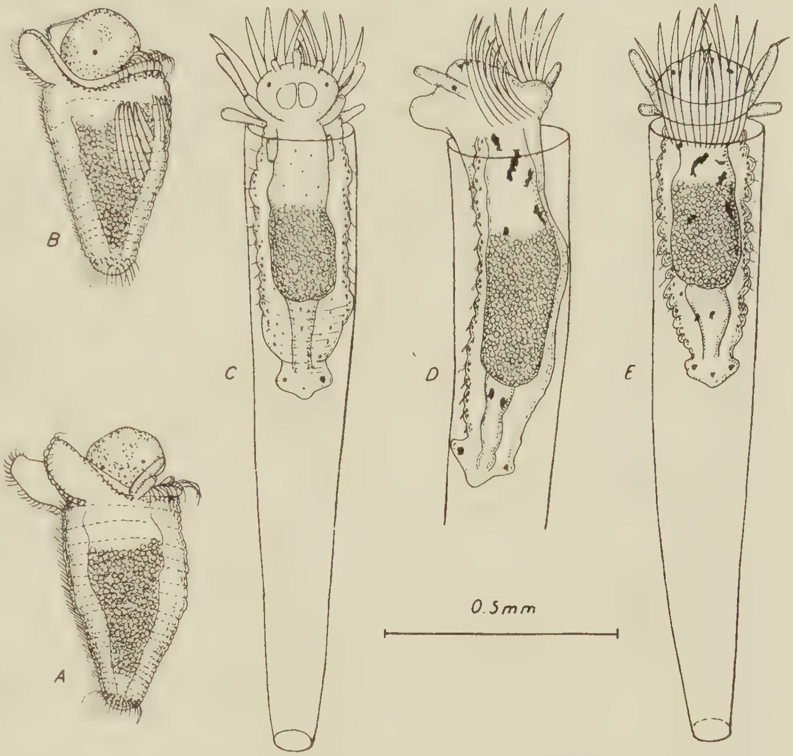


Fig. 63 A-E. *Pectinaria auricoma* Müller. Larvae from plankton off Frederikshavn, NW. Kattegat, drawn from life. — *A*. Young larva with large prototrochal lobes, internal paleae and without tube, seen from the left side. — *B*. Similar larva seen from the dorso-lateral side, with distinct internal paleae (both caught and drawn on $^{3}/_{7}$-1937). — *C* to *E*. Old larva with small prototrochal lobes, external paleae and secreted tube (caught on $^{30}/_{6}$-1937; drawn on $^{1}/_{7}$-1937). — *C*. From the ventral side, *D*. from the right side, and *E*. from the dorsal side (the tube had the same structure of rhomboid plates as is known for *Pectinaria koreni*, but this structure was not sketched here).

B. Own remarks. The criteria given by Sømme to prove the identity of his larvae with *Pectinaria auricoma* seem so good that they may hardly be questioned. Larvae of this type, which in their oldest planktonic stages inhabit long slender slime-tubes, were found in plankton hauls taken off Ven on $^{17}/_{6}$-39 (1 old larva), $^{3}/_{7}$-39 (6 larvae), and off Helsingør on $^{7}/_{10}$-41 (5 somewhat younger larvae). Probably larvae of this species were also seen in the years 1936—37 and 1938, but in these years they were only listed as "*Pectinaria*" without indication of their species. In summer plankton from N.W. Kattegat (Frederikshavn) these larvae were very common, and the figures given here (fig. 63A—E) are based on such larvae from the Frederikshavn plankton. The larvae figured are much younger than those figured by Sømme (l. c.); the youngest stages (fig. 63 A—B), 570—610 μ long, are still without tubes, have internal paleae, are colourless with a bluish-green intestine and black spots of pigment on the head and on the anal segment. The tentacular cirri have already developed, and there are two large prototroch-lobes. The older larvae (fig. 63 C—E), 720 to 920 μ long, which are found in their slender tubes, have paleae on the head like the adults. They are colourless, with green intestines, small spots of black pigment at the base of each parapodium, and large black spots scattered over the body. Two black eyes, three pairs of tentacular cirri, and three antennae.

Pectinaria (Lagis) koreni Mgrn. Northern and middle parts of the Sound, common on sandy bottom at small depths.

Reproduction: A. Literature. Nilsson (1925) reports, from Kristineberg, that the species has separate sexes, that the individual specimens live only for one year, and that spawning takes place in May, June, and July. Wilson (1936a) on April 24th collected ripe animals of *P. koreni* at Plymouth which, when placed in aquaria and removed from their tubes, commenced to spawn. Spawning in a single female took more than two hours. The eggs are tiny, 62 μ across, and the egg-membrane forms part of the larval cuticle. The fertilisation was successful, the larvae swam about 16 hours later, and 3 days old Trochosphaeres were obtained and figured. Older larvae were not reared. Watson (1928) figures larvae (sketched after fixation) and mentions that larvae obtained from plankton off Port Erin, which swam about near the bottom of a glass dish, secreted a transparent tube in the course of one and a half hours. This tube had a faint structure as if joined together of rhomboid plates, it was 1 mm long, largest diameter 0.25 mm (at the mouth), and smallest diameter (at the hindmost end) 0.12 mm. In Kristineberg plankton Nilsson (l. c.) found larvae of *P. koreni* in a state of tube-building in June 1910. These larvae were transparent, had a well developed scapha, 13—14 segments provided with capillary bristles, and 6—7 external paleae on either side of the head. The segment with the paleae and the following segment had well developed tentacular cirri. A black spot of pigment at the base of each parapodium. Tube: 1 mm long, largest diameter 0.20 mm and smallest diameter 0.10 mm. Nilsson figures a very young bottom-stage with the first few grains of sand attached to the mouth of the transparent larval tube. Similar tubes are figured by Watson (l. c.).

B. Own remarks. A male specimen captured off Hellebæk, sandy bottom, 10—20 m, on $^{29}/_{6}$-42, on the same day spawned a large cloud of sperms in the laboratory. The spermatozoa were very active. As mentioned above, the literature gives good clues to the recognition of these larvae in the plankton, and we know them extremely well from our samples taken in the Sound within the last few years. During the first years of our investigation, however, we did not separate them from the other species of *Pectinaria*-larvae. Larvae of *P. koreni* were observed with certainty in the Sound plankton off Ven on: $^{12}/_{7}$-39 (10 spms., with the tube just formed); $^{15}/_{7}$-39 (13 spms., younger as well as older stages); $^{5}/_{8}$-39 (3 older larvae); $^{18}/_{8}$-39 (4 young larvae), and $^{8}/_{8}$-42 (several young larvae), and off Helsingør on: $^{25}/_{10}$-41 (1 spm. with tube); $^{15}/_{5}$-42 (2 very young larvae); $^{20}/_{6}$-42 (2 young larvae); $^{6}/_{7}$-42 (2 young larvae); $^{13}/_{7}$-42; $^{17}/_{7}$-42; $^{18}/_{7}$-42 (8 larvae, young as well as old with the tubes formed); $^{25}/_{7}$-42 (47 larvae, 11 of them with tubes), and $^{17}/_{8}$-42 (6 larvae, young as well as in tubes). As will be seen, all the larvae observed were taken in May to August. The youngest stages (fig. 64 A) are 450 μ long with very large prototrochal lobes and a longitudinal band of cilia along the whole ventral side. The prostomium has brownish-black points of pigment and two black eyes. The prototrochal cilia are placed upon a yellowish-brown base, caudally to which is a reddish-brown pigmentation. Brownish-black pigment on the anal segment. The intestine contains reddish-brown and greyish food-pellets. The next stage (fig. 64 B), 580 μ long, is able to bring the paleae into an external position within less than one and a half hours. The tube — the broad end being formed first — is secreted after the paleae have appeared. The older larvae (fig. 64 C), 725 μ long, with tubes and external paleae, agree closely with the descriptions in the literature. The only point I can add to the description given by Watson and Nilsson (l. c.) is that the foremost and the hindmost parts of the head as well as the sutures between the first chaetigerous segments on the ventral side are provided with reddish-brown spots of pigment. Apart from this the larva is colourless; the intestine is greyish.

A bottle-collector exposed near Ven at a depth of 16 m from $^{17}/_{8}$-39 to $^{22}/_{10}$-39 contained a single young bottom-stage of this species (fig. 64 E). The tube (fig. 64 D) agreed in all details with those figured by NILSSON and WATSON, and as in their sketches, 11 or 12 transparent rhomboid plates could be recognised in each longitudinal row on the larval tube. Anteriorly to this was the first small beginning of the sand-incrusted tube of the adult animal. The animal, hardly more than 1 month after metamorphosis (fig. 64 E), was still very similar to the oldest planktonic larval stages. The characteristic reddish-brown pigmentation was still present, the black spots of pigment at the base of the parapodia were very distinct. The intestine showed the following colours: nearest the mouth colourless with brownish-black food particles; next area with a bluish-green granulation, hindmost area with a yellow granulation and black excrements. Scapha had a somewhat different shape from that of the planktonic stages. — Young larvae in stage I (no tube, internal paleae) may metamorphose into stage II (with tube and external paleae) within a few hours, and they are able to vary the duration of their planktonic stage in accordance with the surrounding conditions (cf. further the discussion on p. 464).

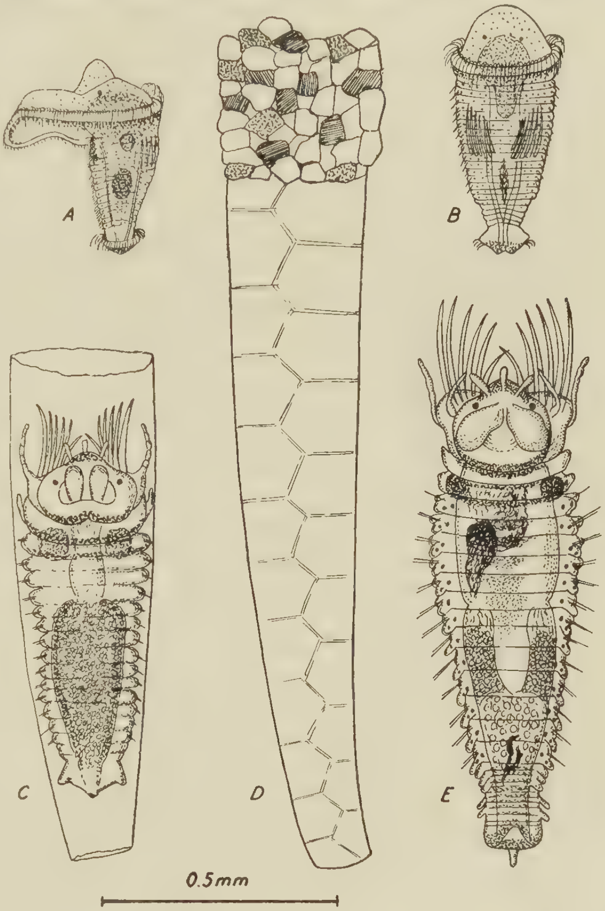


Fig. 64 *A*-E. *Pectinaria koreni* MGRN. — *A* to *C*. Larvae from plankton off Ven, depth 18 to 0 m. — *A* and *B*. Yong larvae with large prototrochal lobes, internal paleae and still without tube (caught and drawn from life on $^{8}/_{8}$-1942). — *C*. Old larva with small prototrochal lobes, with tube and external paleae (caught and drawn living on $^{12}/_{7}$-1939). — *D* and *E*. Young metamorphosed bottom stages from a bottle-collector exposed off Ven, depth 16 m, from $^{17}/_{9}$ to $^{22}/_{10}$-1939. — *D*. Larval tube, with a rhomboid pattern and the sand grain structure characteristic of the adult tube. — *E*. The animal dissected out from the tube fig. D (drawn from life on $^{23}/_{9}$-1939).

Pectinaria belgica PALLAS. Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. NILSSON (1925) states that the tube in *P. belgica* shows the same proportion between length and breadth as that of *P. koreni*. By Kristineberg ripe specimens were found on $^{19}/_{7}$-21, while all specimens examined on $^{4}/_{8}$-22 had spawned their sexual products. NILSSON suggests that the animals will not attain sexual maturity until 3 years after metamorphosis. LESCHKE (1903) figures and describes a larva taken in the Bay of Kiel on $^{2}/_{9}$-01, which he refers to this species. Unfortunately he uses the name *Pectinaria belgica* as synonymous with *Pectinaria koreni*, and his figure gives so few details that it seems very difficult to decide to which of the species of *Pectinaria* his larva should be referred. LESCHKE states, however, that his larva agrees closely with an "unknown larva" described and figured by WILLEMOËS-SUHM (1871) from Hellebæk, and according to our experience from the Sound this larva seems to be a true larva of *Pectinaria belgica* (the scale of enlargement given in the figures of

Willemoës-Suhm seems to be erroneous (cf. my remarks on his figures of *Terebellides strømi* on p. 125 of this paper)).

B. Own remarks. Besides the larval types referred to *P. auricoma* and *P. koreni*, a third larval species belonging to the genus *Pectinaria* is also met with in the Sound plankton. The larva (fig. 65) is much longer than the larvae of the two preceding species in the same stage of development. The young larval stages (fig. 65 A-B), up to 880 μ long, still with the paleae inside and without tubes, are colourless, with small greyish-green spots of pigment on the head and on the anal segment. The intestine has greyish-green granulations. Two black eyes and two very large prototroch-lobes. The older larvae, 1 mm long, with external paleae, inhabit transparent tubes (fig. 65 C), which measure 1.8 mm in length and 0.30 and 0.15 mm respectively in largest and smallest diameters. The tubes had a similar structure of rhomboid plates to those of the preceding species (no figures are at hand of the older larvae). As these larvae are rather common in our plankton, and since in addition to *P. auricoma* and *P. koreni* only *P. belgica* is recorded from the Sound, it seems justifiable to refer the larvae to *Pectinaria belgica*, especially as the three species mentioned are the only common forms of this genus in the Kattegat also. The larva figured by Willemoës-Suhm (1871, fig. 11) seems to agree with our larva of *P. belgica* from the Sound.

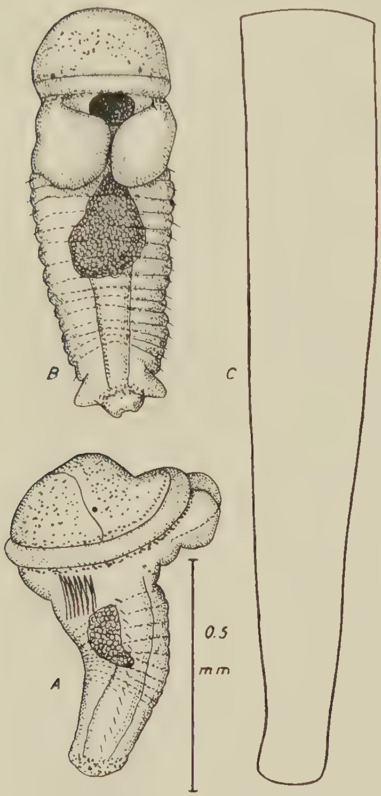


Fig. 65 A-C. *Pectinaria belgica* Pallas. Larvae from plankton off Ven, caught and drawn from life on $^{5}/_{6}$-1938.—*A* and *B*. Young larvae with large prototrochal lobes, with internal paleae, and still without tube,—*A*. From the right side.—*B*. From the ventral side.—*C*. Secreted slime tube of old planktonic larva.The animal inside (not drawn) had small prototrochal lobes and external paleae. The tubes have the same structure of rhomboid plates as in other species of *Pectinaria* larvae.

Larvae of this species in our plankton collections were observed off Ven on: $^{6}/_{6}$-38 (43 larvae in different stages of development); $^{18}/_{6}$-38 (22 spms.); $^{1}/_{7}$-38 (1 spm.); $^{17}/_{7}$-38 (25 spms.); $^{1}/_{8}$-38 (3 spms.); $^{13}/_{8}$-38 (16 spms.); $^{5}/_{7}$-39 (2 young spms.); $^{5}/_{8}$-39 (7 spms., in different stages of development); $^{18}/_{8}$-39 (4 young larvae), and $^{16}/_{9}$-39 (3 young larvae). Off Helsingør no larvae were observed. The larval season is accordingly from June to September, but it occurred earlier in the summer of 1938 than in 1939.

Further remarks on *Pectinaria* larvae.

Besides the larvae which have been referred to the three species of *Pectinaria* mentioned above, several larvae were observed and noted down as "*Pectinaria*-larvae" without any specific name, especially in the years 1936, 1937, and 1938. All these larvae probably belonged to one of the three species mentioned above. In general it can be stated that all the finds of *Pectinaria*-larvae in the Sound, i. e. from all the main-series taken throughout the year, were made in the months from May to October, with a very pronounced maximum in August. Hence all the species of *Pectinaria* known from the Sound are typical summer spawners.

Ampharete grubei MGRN. Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. FAUVEL (1897, pp. 132—34) observed spawning near France at the beginning of March. Ripe females are salmon-coloured, ripe males greenish-white. The ripe ovoid eggs, 100 × 160 μ in diameter, are shed singly in the sea through the nephridia, which have their external aperture just behind the third chaetigerous segment. The external egg membrane swells considerably in the water. The sperm is shed in the same way. The fertilisation was unsuccessful, but a single larva was found in one of the glass dishes. According to the sketch given (l. c. pl. XXIII, fig. 121) the larva is 740 μ long, 340 μ broad, with one ciliated tentacle. Further details are unknown, but the larval type is decidedly non-pelagic.

B. Own remarks. On $^{3}/_{12}$-41 seven adult females of *A. grubei* were secured in the northern part of the Sound between Hellebæk and Kulla Gunnarstorp, 35 m depth, clay bottom. Two of these contained small eggs and the other five contained large, apparently nearly ripe eggs. These eggs (fig. 66) were shaped like a hen's egg, the largest diameter being 210 μ and the smallest 155 μ; they were quite opaque, rich in yolk, and the egg-membrane was very thin (1 or 2 μ). Eggs of this type will probably develop in a non-pelagic way, but nothing has been observed as to the larval development. The wide distribution of this species in high-arctic seas, where, as is well known, the pelagic development is suppressed in nearly all species, seems to support the assumption that the larval development is non-pelagic.

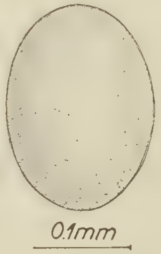


Fig. 66. *Ampharete grubei* MGRN. Ripe or nearly ripe egg taken from adult female, captured between Hellebæk and Kulla Gunnarstorp, depth 30 m, on $^{3}/_{12}$-1941 (drawn from life on the same day).

Ampharete arctica MGRN. Northern and middle parts of the Sound, rather common.

Reproduction: Unknown. However, as in the preceding species, the wide distribution in arctic seas seems to suggest a non-pelagic development.

Anabothrus gracilis MGRN. Northern and middle parts of the Sound, common.

Reproduction: Unknown. Distribution: Common in high-arctic seas. Accordingly the development is probably non-pelagic.

Amphicteis gunneri SARS. Northern part of the Sound, rather common.

Reproduction: A. Literature. FAUVEL (1897, p. 154) states, from France, that the breeding season is in June and that the mode of spawning is just the same as in *Ampharete grubei* (which see), viz. the eggs are shed singly in the sea through the nephridia. The size of the egg is unknown.

B. Own remarks. No observations are at hand from the Sound.

[**Alkmaria romijni** HORST. Unknown from the Sound and the neighbouring seas. Common in the Ringkøbing Fjord (W. Jutland, brackish water) and known from Slien Fjord (between the western Baltic and the Little Belt, brackish water).

Reproduction: A. Literature. This species is insufficiently described and figured by HORST (1920) from the Alkmaarder Meer (Holland). FAUVEL (1927, p. 240) and FRIEDRICH (1938) regard with some doubt the form concerned as a juvenile stage belonging to the genus *Samytha*. Mrs. E. WESENBERG-LUND has (1934) examined about two hundred specimens from

Ringkobing Fjord (preserved in alcohol) and found that they were typical Ampharetids (not Terebellids, as supposed by HORST), which, although closely related to the genus *Samytha*, showed characteristic differences from that species suggesting a separate genus. As the Ringkobing specimens from August—September proved to be viviparous and to protect the young in their tubes, they cannot be regarded as juvenile but must be assumed to be ripe animals belonging to a separate genus. — The three localities from which the species is hitherto known are all brackish. The type of the young (larvae) as well as details on the reproduction are hitherto unknown.

B. Own remarks. During visits at Ringkobing Fjord in July 1939, July 1940, November 1940, and June 1943 I had the opportunity to make some observations on this species and I take the opportunity to mention them here. At depths from one to about five m this worm inhabits the bottom; often 200 adult animals or more occur in a sq.m of bottom. They live in tubes of clay two to three cm long glued together by means of a rust-coloured paste (fig. 67 A). To both sides of the tube adhere externally a thick layer of sausage-like faecal pellets, which often cover a large part of the tube. The living adult animal (fig. 67 B) has eight thread-like slimy tentacles above the broad upper lip and three pairs of subulate gills with transverse rings of greenish-grey pigment. The pharynx, the beating heart over the pharynx, and the intestine are distinct, and, in the summer, eggs of all sizes are seen floating in the body cavity. The hindmost part of the body is very slender and agile. When the animal is placed in a tube of glass instead of clay, the hindmost part of the body will at regular intervals show the same appearance as in fig. 67 C-D, i. e. bending forward to drive the faecal pellets out of the tube.

This species seems to be annual only. In June-July all animals seem to be ripe and have their breeding season, in November all animals were much smaller and without ripe sexual products. Forty to fifty adult living animals examined in July 1939 contained all eggs in the body cavity. Of a similar number of living specimens examined in July 1940 80 to 90 per cent contained eggs, while no sexual products could be seen in the rest, i. e. the smallest of the specimens examined. The botanist Dr. O. HAGERUP has kindly made microtome sections of these latter specimens and placed them at my disposal. They proved to contain large masses of apparently ripe sperm and, among the sperm, a few young but distinct eggs. The species seems thus to be a protandric hermaphrodite and may thus be ranged among the rather small number of hermaphroditic Polychaetes (a list of such hermaphroditic Polychaetes is given by AIYAR & SUBRAMANIAM 1936).

As mentioned above Mrs. WESENBERG-LUND (l. c.) found viviparity in this species. This is in good agreement with the protandry, since there seems to be a relation between viviparity and hermaphroditism in Polychaetes (for instance in *Nereis dumerilii* (partim), *Raphidrilus nemasoma*, *Ctenodrilus serratus*, and *Salmacina dysteri*) or between viviparity and partheno-

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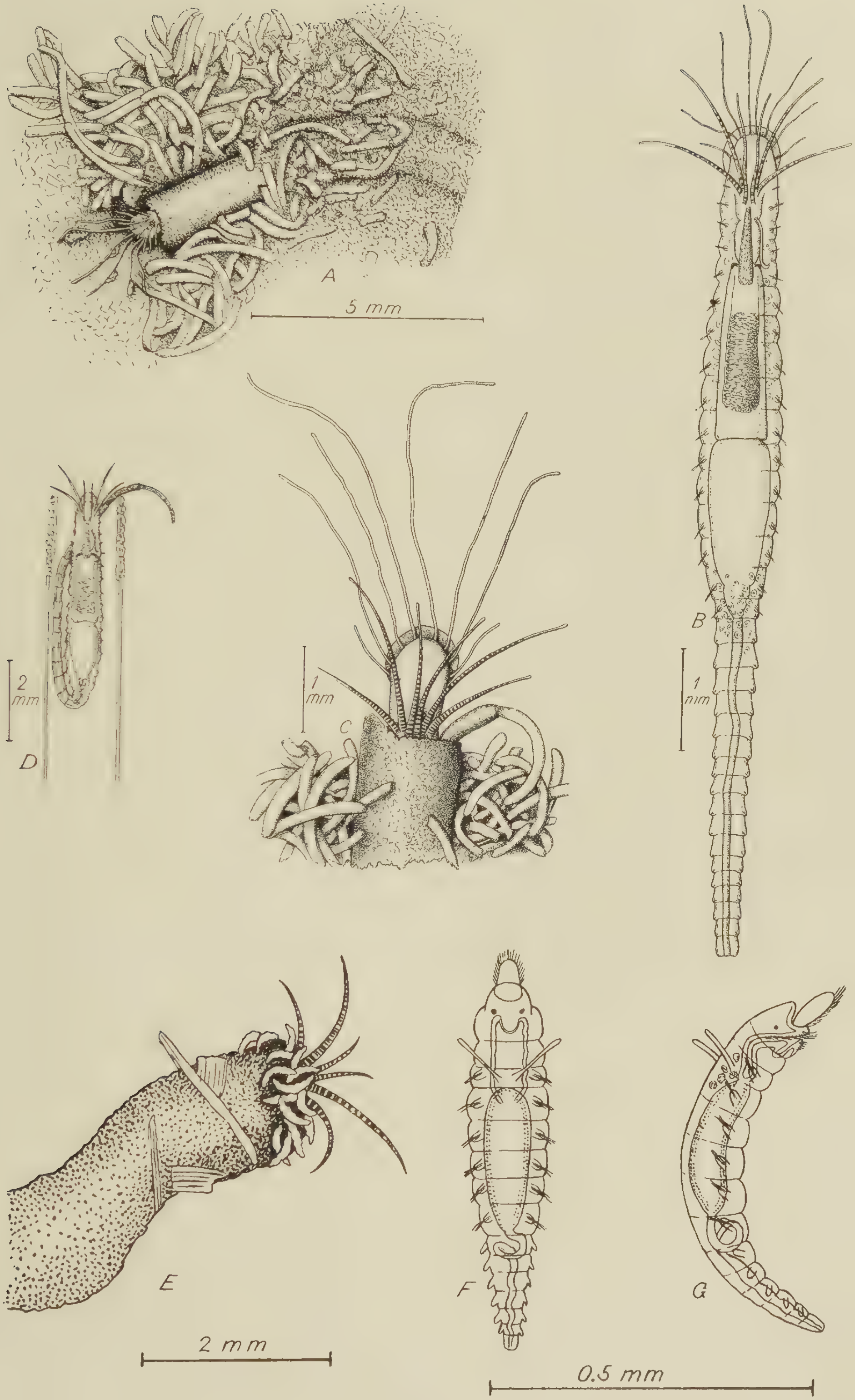
Fig. 67 A-G (see the next page). *Alkmaria romijni* HORST from Ringkøbing Fjord, W. Jutland. — *A* to *D*, caught on $^{6}/_{7}$-1939. — *A*. Adult animal in the act of feeding. Lying in its tube surrounded by its excrements (drawn from life on $^{8}/_{7}$). — *B*. Adult animal seen from the dorsal side (only one nephridium could be seen; drawn living on $^{10}/_{7}$). — *C*. Front part of the animal, staying in its tube with the tentacles stretched out. A faecal pellet is leaving the animal through the anal opening protruding on the right side of the mouth of the tube (drawn from life on $^{8}/_{7}$). — *D*. Adult animal placed in a glass tube, in the act of producing a faecal pellet. The animal has built a muddy wall in front of the glass tube (drawn from life on $^{11}/_{7}$). — *E* to *G*. Caught on $^{13}/_{7}$-1940. — *E*. Adult animal with brood protection. Several whitish young are seen round the mouth of the tube (drawn from life on $^{19}/_{7}$-1940). — *F* and *G*. Young worm (larva) from the tube of the mother animal, seen from the dorsal side (F) and from the right side (G) (drawn from life on $^{19}/_{7}$-1940).


A
5 mm
B
1 mm
D
2 mm
1 mm
C
E
F
G
2 mm
0.5 mm

genesis (for instance in *Syllis vivipara*, *Ehlersia nepiotoca*, and *Dodecaceria concharum*). As no copulation takes place in these worms, it seems reasonable to assume that viviparity is especially connected with such forms as may reproduce by self-fertilisation (hermaphrodites) or without fertilisation at all (parthenogenesis). It is therefore curious that not a single of the specimens examined by me in July 1939, July 1940, and July 1943 showed any signs of viviparity. On the contrary I found that this species is able to reproduce without viviparity. Several of the animals found in July 1940 had 20 to 30 young attached round the mouth of their tubes (fig. 67 E). The difference between the number of young attached to the tube of a single mother animal (20 to 30) and the number of ripe eggs contained in the body cavity of ripe specimens which had not spawned (5 to 95, on an average 57), is so small that the supposition that a pelagic phase with its large waste of larvae might have taken place between spawning and brood protection may at once be excluded. The development is non-pelagic. The appearance of the whitish-transparent young adhering to the tube of the adults (fig. 67 F-G) is also far from what is normally seen in pelagic larvae of sedentary Polychaetes. The first ciliated tentacle is formed, and the first pair of gills have appeared. Parapodia are seen on the first six pairs of the thirteen abdominal segments present. The mouth, pharynx, and intestine, and, in the body cavity, the first small beginning of the gonads are seen. Two black eyes. The only Ampharetid larva hitherto known is, as far as I know, that of *Ampharete grubei* sketched roughly by Fauvel (1897, pl. XXIII, fig. 121) (see this paper p. 121) which seems to agree in broad features with that of *Alkmaria*. — *Alkmaria romijni* seems thus to be an interesting subject for further biological studies].

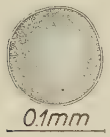


Fig. 68. *Trichobranchus roseus* Malm. Ripe egg taken from female captured off Hellebæk, depth 30 m, on $^{29}/_{7}$-1941 (drawn from life on the same day).

Trichobranchus roseus Malm. Northern part of the Sound, occasional specimens.

Reproduction: A. Literature. Unknown.

B. Own remarks. On $^{29}/_{7}$-41 a female was taken off Hellebæk, at a depth of 30 m, among shells. The animal was quite distended with large, apparently ripe ova, the majority of which were quite spherical and of exactly the same size. The eggs (fig. 68) were rather yolky, and measured from 95—110 μ across, the egg membrane being 4—5 μ thick. It seems impossible from the egg-type and the egg-size to infer whether or not the larva has a pelagic life.

Terebellides stromi Sars. Northern and middle parts of the Sound, extremely common.

Reproduction: A. Literature. Near Naples Lo Bianco (1909) observed both males and females in full sexual maturity from May to November. Willemoës-Suhm (1871) gives the following data regarding the reproduction of this species in the Bay of Kiel: Breeding in May, within a period of two or three weeks. Sexually ripe females are yellowish-green, while the males are milky-white. The eggs are deposited in spherical slimy masses, 4 mm in diameter, attached to the mouth of their own tubes or to decaying pieces of *Zostera*. The individual egg is very small (72 μ in diameter) and develops within the slime-mass into a globular *Trochophora*, which leaves the egg-mass and swims about, rotating slowly, along the bottom. The larvae as well as the eggs (good figures) are of a blackish-brown colour. The larvae have two large red eyes. Willemoës-Suhm figures all stages, even the late *Trochophora*-stage, in which stage the larvae reared by him died. He adds that though he used very fine-meshed plankton nets, he never secured any larvae from the free water masses - a fact which seems to show that the larvae swim directly above the bottom and probably for a very short time only. Leschke (1903), likewise in the Bay of Kiel, sought in vain for these larvae in the plankton, and we may conclude that in spite of their tiny size they have a very reduced pelagic stage, or no pelagic stage at all.

B. Own remarks. During the past years we have been looking for the larvae of this species in our plankton hauls, but in vain, and since larvae, probably belonging to *Artacama proboscidea* (cf. this), are extremely common in spring plankton in spite of their non-pelagic character, it would seem that the larvae of *Terebellides stromi* have a still more non-pelagic development.

Off Kulla Gunnarstorp, depth 30—35 m, hard *Haploops*-bottom, a female quite distended by a large number of pink, ripe eggs (fig. 69) occurred on $^{15}/_{5}$-42. The eggs are not discoidal, but somewhat flattened on two sides and highly opaque. The largest diameter of the egg was 135 μ, i. e. much more than stated by Willemoës-Suhm (viz. 72 μ). The statement by Willemoës-Suhm, that the eggs as well as the larvae are blackish-brown, is likewise peculiar, since our eggs are pink in colour — i. e. in direct light. Willemoës-Suhm may have described the colour which the yolky, intransparent eggs and larvae show when seen in transmitted light; however, this disagrees with his statement that the eyes are red, since this can only be observed in direct light. Is seems at present impossible to solve the problem, but as the adult *Terebellides strømi* is very characteristic and cannot be confused with any other Danish Polychaete, it seems impossible that any errors may have blurred the picture. Hence it seems important to examine these questions in detail as soon as possible.

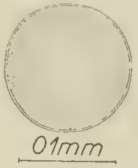


Fig. 69. *Terebellides strømi* Sars. Ripe egg seen in its largest diameter. Drawn from life after dissection from ripe female quite distended by pink eggs; taken between Hellebæk and Kulla Gunnarstorp, depth 30 to 35 m, on $^{15}/_{5}$-1942

[**Nicolea zostericola** (Ørsted). Unknown from the Sound, but common in other Danish waters, e. g. the Little Belt and the Isefjord.

Reproduction: A. Literature. Willemoës-Suhm (1871) and Herpin (1925) describe and figure the spawning-habits, egg-cocoons and development from Kiel and from the French coast respectively. Their results are: Breeding at Kiel from April to June, off France from March to the middle of May. Spawning may take place during all the 24 hours and no connection with the lunar phases was observed. The female may spawn even when no male is present. Normally a ripe male leaves its tube and swims to the mouth of a female tube, resting here upon a net spun by the female. With the male and the female tentacles joined in a common bundle the spawning begins under violent contractions of the bodies. First the sperm is spawned and — a few minutes later — the eggs appear in four strings (two from each side of the body) which are united into one coil surrounded by slime between the tentacles. Twenty minutes later the surface of the slime is hardened into a cocoon attached by slimy cords to hydroids, algae, or other substrata. A ripe female is able to spawn at least three cocoons within a rather short time. The cocoon — 2 × 3 mm — contains several yellowish, opaque, discoidal eggs, 350 μ as the largest diameter. The embryos will not hatch until 7 pairs of parapodia, the first tentacle, and an anterior and a posterior ciliary ring have developed. No pelagic stage. The young worms crawl on the bottom and will soon develop several tentacles and form their tubes.

B. Own remarks. In the northern part of the Little Belt the adults with their egg-cocoons were met with in large numbers attached to colonies of *Flustra* at 40 m depth during the last half of July. The transparent cocoons (fig. 70 A) were often attached to the outer surface of the female tube, and the yolky yellowish-red eggs were distinctly seen. They were only slightly discoidal (fig. 70B), with 240 μ as their largest diameter, thus being much smaller than the eggs measured by HERPIN (l. c.) near France. The large number of egg-capsules contained embryos in all ages, thus also several with advanced embryos apparently ready to hatch (fig. 70C—E). They were whitish, solid, opaque, with four red eyes, one tentacle, two ciliary rings, and showed the first traces of segmentation. However, not a single embryo which had developed the parapodia was observed, and all embryos from the Little Belt — though non-pelagic — seemed to hatch in an earlier stage than those from France, a fact which is in good agreement with the smaller size of the eggs in Danish specimens.]

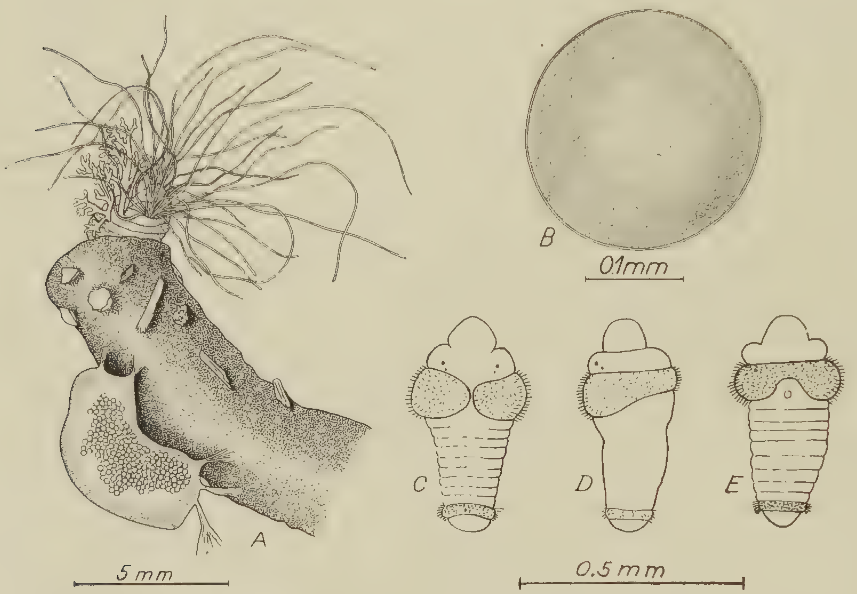


Fig. 70 A-E. *Nicolea zostericola* (ØRSTED). Taken between Middelfart and Strib in the Little Belt, depth 40 m. Caught and drawn from life on $^{31}/_{7}$-1944. — *A*. Female on a colony of *Flustra* with an egg cocoon attached to the outer surface of its tube. — *B*. Undeveloped egg from another egg capsule taken in the same locality and on the same date. — *C* to *E*. Oldest embryos found, nearly ready to hatch. Seen from the dorsal side (C), the right side (D), and the ventral side (E). Same locality and date.

Nicolea venustula MONTAGU. Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. While the reproduction and larval development of the closely related species *Nicolea zostericola* have been studied very thoroughly (WILLEMOËS-SUHM 1871, HERPIN 1925; cf. also fig. 70, p. 126 in this paper), the observations recorded for *Nicolea venustula* are only few and scattered. HERPIN (1925) gives the following details for the latter species: *Nicolea venustula* spawns in a way quite different from that of *N. zostericola*. Near France the latter spawns very large ova, 350 μ across, united in slimy strings which will merge into a cocoon. In the course of a short time, however, *Nicolea venustula* spawns a large number of ova, 250 μ across, which are shed freely in the water and will spread immediately after having been spawned. Nothing is known of the larval development, but DE SAINT-JOSEPH (1906, p. 236) has seen young bottom-stages in the Mediterranean. Such stages with 16 chaetigerous segments and 31 abdominal segments have only one pair of gills.

B. Own remarks. Nothing is known concerning the reproduction of this species in the Sound. The large ova of *Nicolea zostericola* will develop without any pelagic stage. However, also the egg-size in *N. venustula* is considerable, and it seems likely that the pelagic stage — if any — is very short. In our plankton collections no larvae have been found which may be referred to this species.

Amphitrite cirrata Müller. Northern and middle parts of the Sound, very common locally in deep water.

Reproduction: A. Literature. Nothing is known about the reproduction of this species. The only note on the larval development in *Amphitrite cirrata*, by Fauvel (1916b, p. 116) and repeated by Herpin (1925, p. 179), gives, without figures, the following data: A young larva captured off the Azores inhabited a transparent, cylindric tube, but still did not show the slightest development of the tentacles. The abdominal segments showed uncini resembling those of *A. cirrata*, adult specimens of which are abundant within the area in question. It is therefore supposed by the said authors that the larva is a post-larval stage of *Amphitrite cirrata*. — The related species *Amphitrite ornata*, however, has been studied rather thoroughly at Woods Hole (Mead 1897, Scott 1909, 1911), and for the purpose of giving some hints for future investigations on *A. cirrata*, the observations made on *A. ornata* will be briefly summarised here: Ripe specimens in June to August, main spawning in July closely associated with the spring-tide. While still in their tubes, males as well as females spawn their sexual products in thread-like masses from five openings at the front part of the body. The female spawns only the ripe ova, retaining all the unripe ova in the body-cavity. The number of eggs spawned is enormous; their colour is muddy, they are shed freely in the sea and are immediately dispersed by the currents. The egg-size is not given, but young free-swimming Trochophores are figured. The free-swimming period is, however, very short. Thus it is stated that larvae 5 days old are easily kept in glass dishes with *Ulva*, where they will soon loose their cilia and begin to crawl on the bottom. They will leave the plankton when five trunk-segments have developed.

B. Own remarks. A large female of *A. cirrata* secured off Hellebæk, 35 m depth, on $^{11}/_{7}$-41, spawned, while in its tube, a large number of pink eggs of different sizes. Most of them were apparently ripe, being all of the same size, viz. 145 μ in diameter, the egg membrane being 5 μ thick (fig. 71). — A plankton series taken between Hellebæk and Kulla Gunnarstorp, depth 30—0 m, on $^{18}/_{9}$-41 contained a single large Terebellid-larva (fig. 72). Willemoës-Suhm (1871) mentions two types of Terebellid-larvae, viz. those with otoliths, which have a long pelagic larval life, and those without otoliths, which have a very short pelagic life or no pelagic life at all. The larva from the Sound has two distinct otoliths and seems in every respect to be well fit for a long pelagic life. Thus, the type of the larva resembles rather closely that of the larva of *Lanice conchilega* (see below), which has a long pelagic life and lives in thick cylindrical tubes of slime. Our larva is even more similar to the post-larva of *Liomia medusa* (Wilson 1928b, Aiyar 1933). The larva was, however, found without any tube, but quite possibly the larva had left its tube before I discovered it in the plankton. I have often seen *Lanice*-larvae

Fig. 71. *Amphitrite cirrata* Müller. Ripe egg, spawned (and drawn from life on the day of capture) by a ripe female taken on *Modiola*-epifauna off Hellebæk, depth 35 m, on $^{11}/_{7}$-1941.

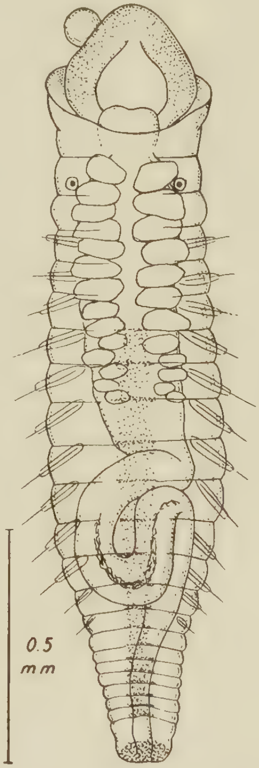


Fig. 72. Larva of *Terebellid sp.*, perhaps belonging to *Amphitrite cirrata* Müller (see the text p. 127). Taken in plankton between Hellebæk and Kulla Gunnarstorp, depth 30 to 0 m, on $^{18}/_{9}$-1941 (drawn from life on $^{19}/_{9}$-1941 after having been placed in a narrow glass tube).

leaving their tubes when placed in Petri dishes, and the same has probably been the case with the larva from the Sound. When I am right in this supposition, it seems to me to be justifiable to refer the larva to *Amphitrite*, because, like that described by FAUVEL, it has reached an advanced stage of development without developing its tentacles. This is, however, merely a supposition and against this tells i. a. the fact that the adult *Amphitrite cirrata* is common in the Sound and that the larva has only been found on one occassion and in a single specimen.

Our larva (fig. 72) is 1650 μ long and 400 μ broad. It is colourless apart from a yellowish-brown pigmentation on the upper lip (sulphur-coloured in direct light), on the anal segment, and along the middle line of the hindmost part of the abdomen. The intestine is light yellow with dark faecalia in the hindmost part. Each chaetigerous segment contains only one bristle on each side. There are two pairs of carmine eyes on the dorsal side of the head, and only the first slight trace of a single budding tentacle is seen.

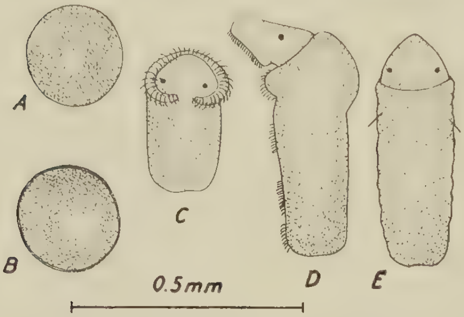


Fig. 73 A-E. *Artacama proboscidea* MGRN. — *A*. Ripe discoidal egg taken from the body cavity of a female from Viken-Ellekildehage, depth 35 to 40 m, on $^{19}/_{12}$-1941. The eggs are pale pinkish, and the egg membrane is very thin. — *B* to *E*. Larvae floating in the plankton between Hellebæk and Kulla Gunnarstorp on $^{27}/_{4}$-1941, drawn from life the next day. — *B*. Still without cilia. — *C*. Barrel-shaped with a ciliary ring and two sealing-wax red eyes. — *D*. Oldest planktonic larva (seen from the left side) of the typical Terebellid-shape (compare the larva of *Nicolea zostericola* fig. 70 C-E). The older larvae are yellowish-white. — *E*. Old larva seen from the dorsal side (with the first pair of bristles).

Neoamphitrite figulus DALYELL. Northern and middle parts of the Sound, in the zone with Baltic water, rather rare.

Reproduction: A. Literature. McINTOSH (1922, p. 121) has examined females in May which had salmon-coloured ovaries crowded with very minute ova. The individual egg measured 46 × 37 μ in longest and shortest diameters respectively. Nothing is known about the larval development, and no observations are known from the Sound.

Artacama proboscidea MGRN. Extremely common on soft bottom in the northern and middle parts of the Sound.

Reproduction: A. Literature. Unknown.

B. Own remarks. Five females of this species taken between Viken and Ellekilde Hage, depth 35—40 m, on $^{19}/_{12}$-41, contained a large number of apparently ripe ova in the body-cavity. The eggs (fig. 73 A) were rather large, discoid, with a very thin egg-membrane, and measured 170—180 μ in largest diameter. They were of a yellowish-pink colour. — In spring plankton from the Sound, Trochosphaeres occur every year in fairly large numbers (fig. 73 C). They are massive, yolky, opaque, and in direct light of a yellowish-white colour. In a later stage of development these larvae, still very massive, are cylindrical with two large red eyes (fig. 73 D-E), and the last stage found in the plankton — a swimming-crawling stage — showed a type of larva probably belonging to the *Terebellidae*. Such larvae are present in our plankton-series taken off Ven on: $^{10}/_{5}$-38 (370 spms., young and older larvae); $^{22}/_{5}$-38 (18 older larvae); $^{17}/_{5}$-39 (20 spms. in all stages of development); $^{4}/_{6}$-39 (10 larvae); $^{17}/_{6}$-39 (one large larva), and off Helsingør on: $^{27}/_{4}$-42 (175 larvae, most of them young), and $^{15}/_{5}$-42 (2 larvae). The large numbers of larvae which occur in the spring plankton in conjunction with the fact that the individual larva of this type will only stay for a very short time in the plankton, suggest that the larvae originate from a species which is very common in the Sound in the adult stage. As already mentioned, the larvae seem to develop into *Terebellidae*, and at first I believed them to be the larvae of *Terebellides strømi*. The papers of Willemoës-Suhm (1871) and Leschke (1903) convinced me, however, that I was wrong in this supposition, the eggs and larvae of *T. strømi* being much smaller than our plankton-larvae and provided with characteristic black pigment. In the Sound the eggs of *Terebellides strømi* are much larger (135 μ in diam.) than at Kiel (72 μ in diam.), and no black pigment was seen on the ripe, pink eggs from the Sound (cf. p. 125). The larvae from the plankton were, however, so different from all figures of larvae of *Terebellides strømi* that I had to look for another Terebellid species which was really common in the Sound. Of such forms only *Artacama proboscidea* may come into consideration. Eliason (1920), records this species as the commonest Polychaete in the Sound besides *Terebellides strømi.* The eggs of *Artacama* and the youngest larvae found in the plankton agree well in volume and colour, and I have no hesitation in referring the larvae found to this species. They are lecithotrophic, i. e. they will feed on their own contents of yolk until reaching the bottom-stage. In a Petri dish they will always swim slowly along the bottom, and their pelagic development should merely be regarded as a short stage of dispersal. — Dr. Blegvad has kindly informed me that on $^{6}/_{10}$-25 he observed two specimens of *Artacama* with ripe sexual products near Lyø-Aarosund, and several specimens filled with eggs were observed in Sejrø Bay on $^{28}/_{5}$-26. Thus the sexual products seem to ripen already in the autumn and to be retained in the body-cavity until the spring.

Lanassa venusta Malm. Northern and middle parts of the Sound, common.

Reproduction: Unknown in the literature. No observations from the Sound.

Thelepus cincinnatus Fabricius. Northern part of the Sound, not very common.

Reproduction: A. Literature. Lo Bianco (1909) has seen females with ripe ova at Naples in August to October. McIntosh (1922, 1924) observed a female with ova in the body-cavity near Scotland on October 16th, and states that a female from the Cape Town (preserved in alcohol) on each side between the 6th and 7th bristle-bundle had a distinct genital aperture. The eggs are shed from the body-cavity directly into the sea through these apertures. The largest ripe eggs found measured 762 μ in diameter.

B. Own remarks. Nothing is known concerning the reproduction in the Sound. The egg-size is, however, so large that it can be taken for granted that the pelagic development is suppressed.

Lysilla loveni Mgrn. One specimen found off Copenhagen, one specimen in the Northern part of the Sound.

Reproduction: Unknown in the literature. No observations from the Sound.

Lanice conchilega (Pallas). The upper part of the characteristic tube of this species was taken off Lappegrunden, depth 20 m, in August 1941. The animal was not inside, but the tube looked so fresh that it would seem that this species lives in the Sound. Dr. Brattström (Zool. Inst., Lund) has informed me that several tubes of *Lanice* have been taken E. of Svinbådan at a depth of 18 m and also in other localities in the northern part of the Sound.

Reproduction: A. Literature. Claparède (1863) has described and figured the larval stages from the French coast near Cherbourgh, taken in July to September 1861. The eggs and youngest stages are unknown; the larvae described by Claparède were all taken

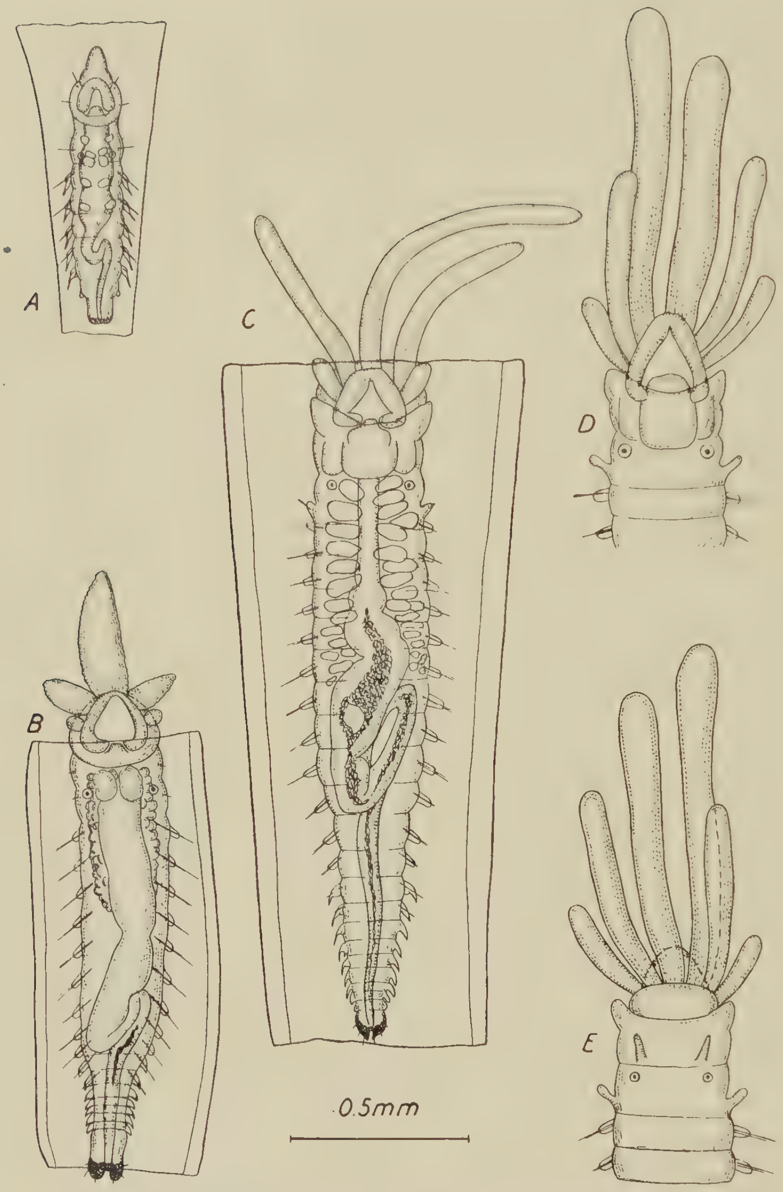


Fig. 74 A-E. *Lanice conchilega* (Pallas).—*A-C.* Larvae from plankton (depth 12-0 m) off Frederikshavn (N.W. Kattegat), all drawn from life immediately after capture on $^{27}/_{7}$-1939. —*A.* Young larva with one tentacle only in its colourless slime tube. —*B.* Larva of intermediate size with five budding tentacles. —*C.* Oldest planktonic stage found, with three long and two small tentacles and with food in the intestine. The slime-tube is now much thicker than in younger stages.—*D* and *E.* Young metamorphosed bottom-stage, placed as old planktonic larva in an aquarium on $^{27}/_{7}$-1939, where it metamorphosed, settled and secreted a slime-tube with sand grains on $^{1}/_{8}$. Drawn from life on $^{8}/_{8}$. —*D.* Front part of the animal seen from the ventral side. —*E.* The same from the dorsal side. The budding gills are seen. Tentacles reddish-brown in their distal ends.

from plankton. The youngest larvae examined, 260 μ long, were just as often found in newly secreted slime-tubes as outside such tubes. Older larvae were always found in their tubes. The two distinct otocysts show that the larva has a long pelagic life. Claparède gives a series of good figures of the larva. Cunningham & Ramage (1888) have figured the same larva from the Firth of Forth, and several other scientists have seen and recorded the pelagic larvae. Giard (1878) records — as *Wartelia gonotheca* — young post-larvae of this species adhering by their tubes to the Hydroid *Laomedea gelatinosa*, and McIntosh (1922, p. 143) states that young bottom-stages which adhered by their tubes to the leaves of *Laminaria digitata* have been found near the low water mark at St. Andrews and Lochmaddy. Herpin (1925, pp. 176—177) discusses the whole literature on this larva. Hofker (1920—22, p. CLXIII) records larvae of this species in all stages of development from plankton taken off den Helder (Holland) in May. His description of the larvae seems to agree well with those of the other authors.

B. Own remarks. Two larvae like those fig. 74 B and C were taken off Snekkerslen, depth 20—0 m, on $^{21}/_{8}$-1938. If the adult tubes (see above) had been derived from living animals, which seems the most probable, it is likely that the stock in the Sound is recruited from a few old "drift-larvae" from the Kattegat just ready to metamorphose. In N.W. Kattegat (Frederikshavn) the larvae of *Lanice conchilega* are very common in summer plankton. The drawings (fig. 74 A—E) are all from

Frederikshavn, where I found larvae in large numbers late in July, and Dr. Kramp has told me that he has observed such larvae in the same locality in summer-plankton during several years. Larvae were found in the plankton in all stages from 780 μ (fig. 74 A) to 2600 μ (fig. 74 C) in length, and old larvae metamorphosed in our aquaria (fig. 74 D—E).

The thick-walled slime-tubes are somewhat conical and quite colourless. The young larvae are nearly quite colourless apart from the pale olive-green intestine and the faint brownish anal pigment. The older larvae (fig. 74 C) have yellowish-brown tentacles and eyes, and — on the ventral side — yellowish-brown rows of glandles, which secrete the slime for the tube. The olive-green intestine has now blackish-green contents, the anal segment is still reddish-brown, and each parapodium contains two or three chaeta, which apparently adhere to each other by their distal ends. It is easily seen that larvae of this type are fit for a long pelagic life, and the rapid growth and considerable development of the larval stage show that this is indeed a fact. Statocysts are distinct in all planktonic stages. The larvae have better chances for spreading with the sea-currents than most other Polychaete-larvae.

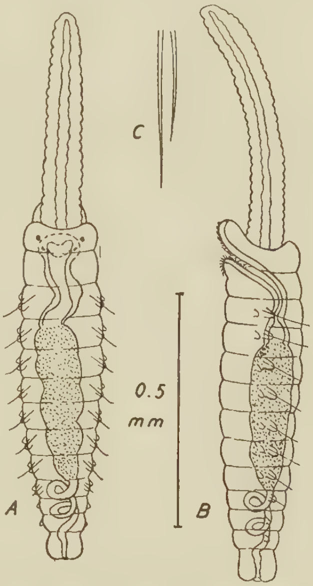


Fig. 75 A-C. Larva of a *Terebellid sp.* From plankton off Ven, 18 to 0 m, caught and drawn from life on $^{1}/_{8}$-1940.—*A*. Larva seen from the dorsal side and *B*. from the left side. — *C*. Capillary bristles highly magnified.

Pista cristata (Müller). Off Hellebæk, depth 20—30 m, shells, on $^{20-30}/_{7}$-41, one well preserved and two somewhat fragmentary adult specimens.

Reproduction: Unknown in the literature. No observations from the Sound.

Other Terebellid-larvae. A plankton series taken off Ven, depth 18—0 m, on $^{1}/_{8}$-40 contained a single Terebellid-larva of a species which had never been observed before in our samples, and which we did not meet with in the plankton during the following years either. The specimen (fig. 75 A—C), 730 μ long from the anus to the base of the tentacle, had eight chaetigerous segments, two pairs of black eyes, and a single tentacle nearly just as long as the whole body. The larva was quite colourless with a yellowish-brown intestine. Only capillary bristles were observed. Apart from the cilia round the mouth not a single band of cilia was present, nor were any other organs found that might serve in the locomotion of the larva, which thus floated passively about in the water. This as well as the whole structure of the larva and its very rare occurrence in the plankton seems to point to a non-pelagic development — the larva simply floats near the bottom for a few days before finally settling. The larva bears a close resemblance to those of *Nicolea zostericola* (Herpin 1925, fig. 106), and *Polymnia nebulosa* (Claparède & Metschnikoff, 1869, fig. 1 E, as *Terebella meckelii*), both of which have no pelagic development in the ordinary sense of the word, but float for some hours near the bottom before settling. — Two bottle-collectors exposed off Ven at a depth of 16 m (2 m above the bottom), from $^{21}/_{7}$ to $^{8}/_{8}$-40 and from $^{24}/_{7}$—$^{13}/_{8}$-40 respectively, each contained one specimen of our larva which had just settled. These two young bottom-stages inhabited thin mucous tubes covered with clay. They measured 200 μ more in length than the larva shown in fig. 75, had nine chaetigerous segments (the larva had eight), and small contents of detritus in the yellowish-brown intestine. Apart from these few facts the two bottom-stages agreed so well with the larva in question, that nothing can be added to the description given above. — I have not the slightest idea as to which species within the *Terebellidae* this larva should be referred, but older stages that may be found in bottle-collectors in the years to come will probably solve the problem.

Fabricia dubia E. Wesenberg-Lund (= **F. sabella** (Ehrenberg) partim). Common in shallow water throughout the Sound.

Reproduction: A. Literature. McIntosh (1923, p. 267) writes on this species "... the sexes are separate. In August the males in the Gouliot caves of Sark had the coelom filled with nearly ripe sperm". De St. Joseph (1894) found a young bottom-stage, 740 μ in length, with large, black anterior eyes and with two eyes on the anal segment. Allen (1915) mentions breeding in February near Plymouth.

B. Own remarks. Mr. Erik Rasmussen has kindly informed me that he has studied the reproduction of this species, which is non-pelagic, in the Copenhagen harbour and in the Isefjord. His detailed observations will be published later.

Laonome krøyeri Mgrn. Northern and middle parts of the Sound, not rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Sabella pavonina Savigny. Rather common, especially in the northernmost part of the Sound.

Reproduction: A. Literature. Lo Bianco (1899, p. 491) states that the rose-coloured eggs were deposited at Naples in April. McIntosh (1922, p. 230) found eggs in the coelom in October. Allen (1915) states that breeding takes place at Plymouth in August and September. Orton (1914b, p. 316) found that *Sabella pavonina* secreted a tube 12.6 cm long in less than 31 weeks, and at this state contained well developed, but not quite mature ova.

B. Own remarks. Nothing is known about the reproduction of this species in the Sound.

Chone infundibuliformis Krøyer. One adult specimen was found within the triangle Helsingør-Hittarp-Hellebæk on $^{7}/_{7}$-41, depth unknown.

Reproduction: Unknown in the literature. No observations from the Sound.

Euchone papillosa Sars. Northern and middle parts of the Sound, common.

Reproduction: Unknown in the literature. No observations from the Sound.

Dasychone bombyx (Dalyell). Recorded by Levinsen from Hellebæk in 1893 as *Dasychone Dalyellii*, and found again in recent years (kind information from Dr. Eliason, Göteborg).

Reproduction: A. Literature. According to Fauvel (1927, p. 319) the species mentioned by Levinsen as *Dasychone Dalyellii* is identical with *D. bombyx* (Dalyell). Dalyell himself (1853) gives the following data as to his species: "Spawning takes place in May-June and August-September, the white eggs are immersed in the thinnest gelatinous matter". This would seem to mean that the eggs adhere to each other imbedded in a very thin mucus. The closely related species *Dasychone lucullana* Delle Chiaje, which is regarded by many authors as synonymous with *D. Dalyellii* (cf. McIntosh 1923, p. 278) has been carefully examined by Claparède & Metschnikoff (1869, beautiful figures), Roule (1887), Carlgren (1900), and Lo Bianco (1899). Their main results concerning the reproduction and the larval development are: At Naples and Marseilles the eggs, imbedded in slime, are situated in a thick mucous ring round the mouth of the tube of the mother animal. The hatching larvae, 220 μ long, are monotrochous and will not develop a second ring of cilia. They have two distinct eyes, two velum-like gill-lobes, and soon after three chaetigerous segments will develop. Claparède & Metschnikoff (l. c.) figure also the somewhat older stage with eight tentacles, but they do not mention whether or not these stages are pelagic. Their type, however, seems to be non-pelagic. This agrees well with a remark of Lo Bianco (l. c.), viz. that the hatching larvae will settle at once near the adults.

B. Own remarks. Nothing is known concerning the reproduction in the Sound.

Myxicola (Leptochone) infundibulum (Renier) — **M. steenstrupii** Krøyer. Rather common in the northern part of the Sound.

Reproduction: A. Literature. Claparède (1870) figures the sperms, but not, as stated by McIntosh (1923, p. 315), both sperms and ova. Nothing is known concerning the breeding time. Caullery & Mesnil (1920) have observed asexual reproduction in the related species *Myxicola dinardensis.*

B. Own remarks. Nothing is known about the reproduction in the Sound.

Potamilla reniformis (O. F. Müller). Recorded from Ven by Levinsen in 1893; not found later.

Reproduction: A. Literature. De St. Joseph (1894) states that the eggs are greyish. Nothing else is known about the reproduction. — Fauvel (1916 a) observed brood-protection in a related species, *Potamilla antarctica.* Between the gills and the front part of the body some specimens contained two large egg-masses in which the embryos may develop to a stage with two eyes and four chaetigerous segments (figured by Fauvel). — Caullery & Mesnil (1920) found asexual reproduction in another species, viz. *Potamilla torelli.*

B. Own remarks. Nothing is known about the reproduction in the Sound.

Pomatoceros triqueter Linné. Northern and middle parts of the Sound. Very common locally at fairly great depths.

Reproduction: A. Literature. Lo Bianco (1909) found ripe specimens at Naples in March and April. Allen & Nelson (1911) reared artificially fertilised eggs at Plymouth, which settled and adhered to the sides of the jars on October 1st, i. e. 33 days after fertilisation. Von Draschke (1884) and Segrove (1941) studied this species by Heligoland and S. England respectively and made the following observations: The males are ten times as numerous as the females. The sperm is whitish, the eggs reddish-purplish, which colour is also characteristic of the ripe female. Spawning in July (Heligoland) and the whole year round with a maximum in March—April (S. England). Artificial fertilisation is easily performed. The reddish-purplish eggs are lens-shaped and very small (largest diameter 75 to 86 μ, smallest diameter 44 μ). Three days after fertilisation the *Trochophora* is developed, i. e. the whole intestine is formed and the larva begins to feed on the plankton. At Heligoland larvae derived from artificially fertilised eggs died 5 days old; all later larval stages described were taken from plankton in July, when they were very scarce in spite of the great abundance of the adults. From the middle of August no larvae were found in the plankton. The oldest pelagic larvae derived from plankton measured 380 μ in length, they had two eyes, three chaetigerous segments, and a few transverse bands of navy-blue pigment (v. Draschke gives good figures of eggs and larvae). The same author states (translated from the German): "The fact that I never found stages more advanced in development, in spite of zealous search for weeks, makes me believe that these animals will sink to the bottom very early and will secrete a slime tube, precisely as described by Milne-Edwards for *Protula*". Segrove (l. c.) has followed the whole development and metamorphosis in culture dishes with *Nitzschia*. The pelagic stage lasts three weeks in summer (more than two months in winter). Six to seven days after metamorphosis the young Trochosphere (100 μ long) has attained a length of 200 μ and in its oldest pelagic stages attains a length of 320 μ. Between the pelagic and the tube-building stages there is a critical crawling stage on the bottom. The larvae in the oldest pelagic stage are positively phototactic (cf. the discussion on pp. 460—463) and settle and secrete their tubes just below the water line. During metamorphosis the larva will shrink to nearly half its size. Dons (1927) has studied this species at Trondheim and says that the youngest sessile stages found have tubes 800—1200 μ long, with animals about 500 μ long. He figures such a young animal which had still some larval characters intact, with two chaetigerous segments and about 20 ciliated tentacles. Animals one year old have tubes 16—18 mm long, two-year old animals have tubes 30—39 mm long, etc., — the species lives for at least four years. Orton (1914b), however, says that this species "grows to a nearly full size in about 4 months, and at this age . . . has in many cases yielded practically 100 per cent of embryos on being artificially fertilized". Fuchs (1911), finally, states that the rearing of Serpulids, especially *Pomatoceros*, in a laboratory is very easy, and he adds that this species "breeds naturally and in great profusion in the tanks at Naples, the young worms settling down and forming their tubes without having any care bestowed on them". McBride (1911) has reared the young of *Pomatoceros* until the larvae attained the adult condition and had formed their tubes, which were attached to the sides of the vessel.

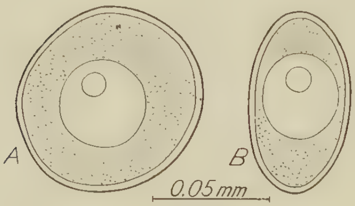


Fig. 76 A-B. *Pomatoceros triqueter* Linné. Uncleaved eggs just spawned by a female taken on Knähaken, depth 30—35 m, on $^{19}/_{7}$-1945 (drawn from life the same day). Seen in its largest (A) and smallest (B) diameter.

B. Own remarks. Five out of seven adult animals caught on Knähaken, depth 30—35 m, on $^{19}/_{7}$-45, spawned their eggs (fig. 76 A—B) on the day of capture when placed in glass dishes, and also from N.W. Kattegat (Frederikshavn) observations of females which spawned their reddish-purplish eggs in the month of July if placed in aquaria are available from several years. The eggs (fig. 76 A—B) are shed singly and will probably spread in the water under natural conditions. Four bottle collectors exposed off Ven at a depth of 16 m (placed 2 m above the bottom) from $^{5\text{-}7}/_{7}$-39 to $^{23}/_{8}$—$^{2}/_{9}$-39, i. e. six weeks on an average, each contained more than one thousand small tubes of *Pomatoceros*, which adhered to the glass-walls or to the cork-floats (2 and 3 m, respectively, from the bottom). Forty-three of these tubes, measured at random, had a length of 2.0—6.5 mm, most of them ranging between 2.0 and 4.0 mm, and had thus grown to this size in less than six weeks. A bottle-collector exposed at the same depth and in the same locality from $^{17}/_{9}$-39 to $^{21}/_{10}$-39, i. e. for five weeks, contained only a few tubes of this species, and precisely the same was the case with three bottle-collectors exposed (same depth and same locality) from $^{27}/_{5}$-41 to $^{17\text{-}20}/_{7}$-41. These facts seem to show that the main spawning normally sets in very suddenly, lasting for a few days only, in the last half of July or the first half of August. The negative result with bottle-collectors in July-August 1940 seems, however, to show either that some variation in the breeding time may occur from year to year, or that the spawning fails to appear in certain years. Several adults taken off Kronborg near Helsingør on $^{4}/_{7}$-41 were all without ripe sexual products. — The pelagic life in the Sound seems to be very short.

Hydroides norvegica (GUNNERUS) = **H. pectinata**. Two beautiful specimens with characteristic opercula were captured at Knähaken, depth 25—35 m, *Modiola*-epifauna, on $^{8}/_{7}$-42.

Reproduction: A. Literature. Breeding near Plymouth in August (ALLEN 1915, p. 644). Good results by artificial fertilisation. Cleavage total, unequal. Larvae, resembling those of *Pomatoceros*, not figured (SOULIER 1898). The young bottom-stages are sexually ripe from four months (at Plymouth, ORTON 1914 b, p. 316) to nine days (at Madras, India, PAUL 1937) after settling.

B. Own remarks. Nothing is known concerning the reproduction in the Sound.

Serpula vermicularis LINNÉ = **S. infundibulum** D. CH. Three adult living specimens adhering to shells of *Cyprina islandica* were taken off Hellebæk, depth 30 m, on $^{14}/_{7}$-41. One further specimen was taken in the same locality and at the same depth on $^{12}/_{9}$-41.

Reproduction: A. Literature. SOULIER (1898 and 1901) has studied the embryology of this species near Cette: sexually ripe all the year round with a maximum in the spring and a minimum in the winter. Artificial fertilisation successful throughout the year. Optimal temperature for larval development 12—15° C. The cleavage is total. Gastrulation 10 hours and *Trochophora*-stage 15 hours after fertilisation. The *Trochophora* has two rings of cilia, one before and one behind the mouth and a tuft of cilia at the anterior end. The figures (in paper from 1901) show that the larva closely resembles that of *Pomatoceros triqueter*, and accordingly the pelagic stage, if any, must be rather short. — ORTON (1914 b) found at Plymouth that "ripe *Serpula vermicularis* not more than about 10 months old yielded an excellent result on being fertilized", and ALLEN (1915) states for the same locality that ripe specimens occur in August-September.

B. Own remarks. An adult male taken off Hellebæk, 35 m, on $^{12}/_{9}$-41, in the aquarium, when removed from its tube, spawned spirals of sperms from all segmental organs. The spawning took several minutes. Nothing known about eggs or larvae from the Sound.

Miroserpula inflata DONS. Northern part of the Sound, rather common locally on stones and shells in deep water.

Reproduction: A. Literature. DONS (1933 b) has studied the growth and reproduction and figured the larva of this species. The orange-coloured, yolky eggs, 180 μ in diameter, are deposited in one or more pairs of "ovicells" secreted by the parent animal on the dorsal side of its calcareous tube near the mouth. When the eggs are found inside the "ovicells", these are closed by a calcareous membrane, and the eggs grow in these breeding-rooms to fully developed *Trochophora*-stages, shaped like a hen's egg, 200 μ long, with a "collar", a transverse band of cilia anteriorly to the mouth, and two large eyes, thus bearing a close resemblance to other Serpulid-larvae figured and described by earlier authors. Up to five pairs of "ovicells" may occur on a single tube. The pair of ovicells nearest the mouth may, for instance, contain quite young eggs, those posteriorly to these may contain eggs in a late stage of cleavage, the next pair of "ovicells" may contain fully developed Trochophores, and the following, older pairs may be empty. This seems to show that the breeding season is rather long. DONS has shown that sexual maturity may be attained in specimens one year old, but supposes that most of the specimens will not commence their breeding until the second year.

B. Own remarks. BRATTSTRÖM & THORSON (1941) mention two localities for this species, both in the northern part of the Sound. One more locality may be added here, viz. a locality off Hellebæk, 35 m, on $^{12}/_{9}$-41, 3 specimens, one of them with a single pair of ovicells, attached to a large slag.—Off Knähaken, 25—35 m, *Modiola*-epifauna, on $^{8}/_{7}$-42, 7 specimens with one pair of ovicells each were found. Two of the specimens in a single ovicell contained embryos ready to hatch together with nearly undeveloped eggs (fig. 77 A), — a fact which is at variance with the observation of Dons (l. c.). Four specimens contained larvae ready to hatch in their ovicells, and a single specimen had exclusively newly shed eggs. Specimens with more than one pair of ovicells have not hitherto been found in the Sound. In a specimen taken W. of Kulla Gunnarstorp and sent to Dons for verification, *Trochophora*-larvae were found in the ovicells. — The larva (fig. 77 B—C) is 210 μ long, has two red eyes, and reddish-brown nutrient globules in the intestine; the body is colourless, a "collar" of cilia is present anterior to the mouth, and a ventral, longitudinal band of cilia is seen. This seems to prove that a pelagic stage, like that known for other Serpulid-larvae, is either totally absent or much reduced, but the hatching larvae have never been followed until metamorphosis.

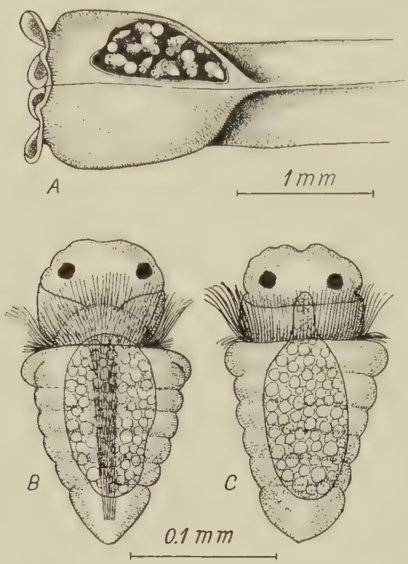


Fig. 77 A-C. *Miroserpula inflata* Dons. —*A*. Front end of tube of adult specimen with one pair of ovicells. One ovicell is opened to show the eggs and embryos inside. Off Knähaken, depth 25 to 35 m, attached to a shell of *Modiola modiolus*, caught and drawn from life on $^{8}/_{7}$-1942. — *B* and *C*. Largest embryo found in the ovicells in fig. A, seen from the ventral side (B) and from the dorsal side (C).

Filograna implexa Berkely. Northern part of the Sound, rare.

Reproduction: A. Literature. McIntosh (1923, p. 242) gives the following data: The eggs are red. The spermaries seem to develop a little later than the ovaries. Gradually they fill the non-bristled region in front of the ovigerous segments and bulge laterally, the region being thus characterised by its pallor. Faulkner (1930) has studied the asexual as well as the sexual reproduction in this species with the following result: "Buds are abundant during spring and summer. Sexual individuals are mature (⚥), and buds rarer during summer and autumn . . . .". "The eggs develop in the calcareous tubes of the parent until the embryo is almost ready to settle. Embryos developed during early summer enter a sexual phase in the same season, those produced later reach their first reproductive phase (asexual) next spring. Individuals last more than one year, hence after a sexual phase there is a return to asexual reproduction in the next spring". Cunningham & Ramage (1888) figure a larva of this species. The larva has three chaetigerous segments, a "collar", a transverse band of cilia, two large eyes, and resembles so closely other Serpulid-larvae that larvae of this type will be very difficult to refer to their species when met with in the plankton. Allen (1915) records breeding near Plymouth in July-August-September. McIntosh (1923, p. 343) states, from Scotland, that "early trochophores of a deep red colour occurred in the glass vessels of sea-water on the 9th of June, the prototroch being visible on each side. They simply rotate or swim in small circles, but the larvae with commencing segmentation of the body dart through the water with great vigour, and often in a straight line, whilst others make larger circles near the bottom. One of the latter showed three segments behind the head, and in all the two eyes were distinct". McIntosh (1913) discusses the possible identity of the species *Filograna implexa* and *Salmacina dysteri*. If these species are identic, the reproduction within the species is much more variable than hitherto described. This variation comprises a different distribution of the sexual products in the buds as well as a varying size of the eggs from locality to locality.

B. Own remarks. Nothing is known about the reproduction of this species in the Sound.

Spirorbis borealis DAUDIN. Common throughout the Sound, especially attached to *Fucus* in shallow water.

Reproduction: A. Literature. WILLEMOËS-SUHM (1871) has examined this species (under the name of *S. nautiloides*) from the Sound and states that the adults are hermaphroditic with reddish-yellow eggs, which, in June, are deposited in a double-cord of slime within the tube of the mother animal. Here the eggs develop into embryos, one of which is figured by the author. CUNNINGHAM & RAMAGE (1888) figure a string of eggs and state that "the embryos were well advanced in development before hatching". LESCHKE (1903, from Kiel, breeding season June) mentions that the "hermaphroditic males" have their eggs in the anterior and the sperms in the posterior part of the body-cavity. He describes the larva inside the tube of the mother animal, where it stays until four tentacles have begun to develop. In this stage "the animal leaves the tube of the mother in the evening, swims freely about during the night, to settle at day-break, when it immediately begins to secrete a calcareous tube. Thus the whole nomad-life lasts for 8 to 10 hours only" (translated from the German). NILSSON (1925) near Kristineberg found that in the autumn of the year in which it is born this species will reach a size of $2^1/_2$ to 3 mm across the whorls of the tube; next spring (3 to $3^3/_4$ mm across) it will spawn (larvae in the mother tube already in May) and then die. FEWKES (1885) describes the development from Newport, U.S.A., and gives a series of detailed and clear figures of the embryo, larvae, and young bottom-stages. According to FEWKES, the brick-coloured larvae when hatching from the tubes of the mother animals will swarm at the surface of the water, and when metamorphosing they are able to float on the surface while secreting the first thin case in which they live. "They float on the surface for a short time until the increasing specific gravity of their bodies sinks them to their future homes". Nothing is mentioned concerning the space of time spent in the plankton. At Woods Hole MARY SHIVELY (1897) noted two breeding seasons: Medio June to medio July, and August. The egg-string is placed outside the dorsal furrow of the cylindrical body of the mother animal, and each string contains 1 to 4 rows of brownish-orange eggs in a number of 10 to 15 per row. Only three days passed from fertilisation to the hatching of the larvae (in contrast to GARBARINI's observation; see below), and two days from hatching to settling. The hatching larva is figured and is of the normal Serpulid-type. At Concarneau and Roscoff GARBARINI (1933, 1936) made the following observations on this species: The number of embryos which develop simultaneously within the tube of a single mother animal is about 20. At a temperature of 11° to 18° C. they take about 14 days from fertilisation to hatching (cf. the results of SHIVELY); at temperatures below 10° C., however, the development is much more retarded, and accordingly the breeding is stopped from December to May. The emission of larvae from the parent-tubes follows a very distinct rhytm corresponding to the lunar phases. Each emission lasts for two to six days, and a few hours after the emission the mother animal spawns a new egg-string, the young of which hatch a fortnight later.

B. Own remarks. On $^{26-27}/_6$-41, 202 adult specimens were examined in a living state at Aalsgaarde, north of Helsingør. Of these specimens 190, i. e. 94 per cent of the number examined, contained in their tubes double egg-strings either with dark-brownish eggs (cf. fig. 78 A) or with yellowish-reddish-brown larvae with two large eyes. In several of these egg-masses the embryos hatched during the observation and swam lively about in the water. On the same dates and in the same locality the leaves of *Fucus serratus* were covered with large numbers of quite small tubes of *Spirorbis borealis* (the largest of them measured $^{1}/_{2}$—1 mm in diameter across the whorls), which had undoubtedly settled only a short time before. There can hardly be any doubt that they belong to an earlier generation of young produced in the same summer. On $^{1}/_{7}$-41 several adult animals were examined at Helsingor. Most of them contained eggs or young. On $^{15}/_{9}$-41 a large number of animals attached to *Fucus* were examined in the same locality. At least 90 per cent of the large tubes found here were empty, but were now often inhabited by young *Polydora ciliata*. The few large tubes which still contained living *Spirorbis* had neither eggs nor embryos. Only in one case was a single free larva of the common appearance found in a tube together with the mother animal. The young specimens of *Spirorbis* attached to the same leaves were all alive, but 50 young animals examined contained not a single egg or young in their tubes. On $^{2}/_{4}$-42 15 specimens adhering to leaves of *Laminaria* were examined at Helsingør. Nearly all of them contained large ripe eggs in the body cavity, and a few of them had already strings with undeveloped eggs in their tubes. These observations, compared with those recorded in the literature, seem to show that the species spawns in spring and summer, when several generations of young are produced. The young will not reach sexual maturity until the spring after the year in which they have been born, and the spawning specimens will normally die when the breeding season is over. — In Isefjord, on $^{5}/_{6}$-43, the first generation of larvae from the same summer had just settled on the algae and had formed their tiny calcareous tubes.

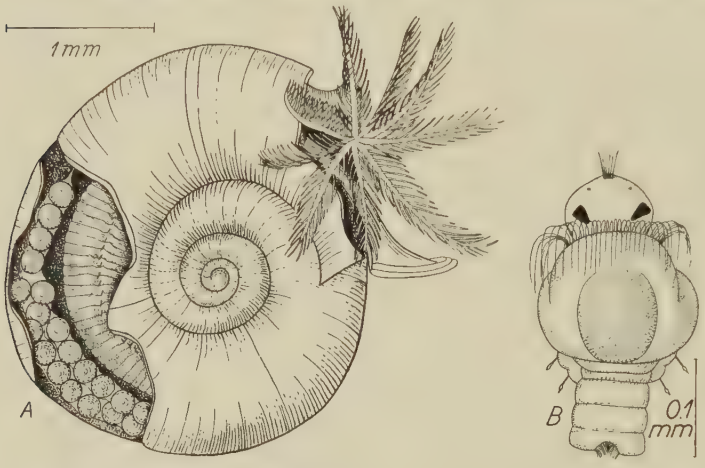


Fig. 78 A-B. *Spirorbis borealis* Daudin. — *A*. Adult animal. The tube is opened to show the double chain of eggs lying close to the body of the mother animal. Taken on *Fucus* near the shore off Helsingor, on $^{23}/_{5}$-1942 (drawn from life the same day). — *B*. Larva just hatched from the tube of the mother animal (yellowish-brick-red with carmine eyes). Seen from the dorsal side. Gamborg Fjord (near the Little Belt), caught and drawn from life on $^{7}/_{7}$-1944.

The hatching larvae (fig. 78 B) are brick-coloured, have two large and two small red eyes, a tuft of cilia in front of the head, a prototroch, and two pairs of lancet-shaped bristles. In our main series only a few small larvae were occasionally observed in the Sound plankton. Such larvae have, however, been listed as "indeterminable larvae of Polychaetes", and they are of no importance at all in the plankton.

Spirorbis spirillum (Linné). Rather common on *Laminaria* at fairly great depths in the northern part of the Sound.

Reproduction: A. Literature. McIntosh (1923, p. 395) writes: "Ova in various stages of development occur in the caelomic cavity of females in summer, and nearly ripe sperms in the males at the same time". Thus the species is not hermaphroditic. Agassiz (1867) figures a part of the egg-string of this species and states that the dark, reddish-brown eggs are laid in strings between the body of the mother animal and the wall of the tube, i. e. not in the operculum. The pelagic life of the hatching larvae lasts only for 8—10 hours. "The young are quite advanced within the body of the parents, previously to the transfer of the egg-sacs to the cavity of the tube, where they complete the greater part of their growth". The larvae always leave the tube of the mother animal in the night, and are then in a stage of development which is very near metamorphosis. "It frequently happens during the night that the smooth sides of the vessel are completely covered with small limestone tubes, formed by the young *Spirorbis* hatched since the evening before". The statement of MARY SHIVELY (1897), that this species has brood-protection in the operculum, does not agree either with AGASSIZ's statement or with our own observations from the Sound. It is quite possible, however, that this species is able to vary its mode of brood protection, this being apparently the case in *Spirorbis granulatus* (see below), but it seems more likely that the observations of SHIVELY refer to another species.

B. Own remarks. Adult specimens with their elegant, regularly twined shells, were common on *Laminaria* at depths of 16 to 18 m off Helsingør on $^3/_7$-41. In 7 out of 10 specimens examined chains of embryos were found inside the tube between the body of the mother and the wall of the tube (fig. 79). The embryos were 180 μ long, yellowish-red, with two red eyes, and five animals, which were more thoroughly examined, each contained between 40 and 50 embryos in their tube.

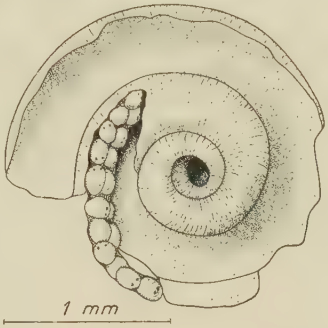


Fig. 79. *Spirorbis spirillum* (LINNÉ). Tube of adult specimen. The animal is removed and the tube opened to show the double chain of embryos. Taken off Helsingor, depth 16-18 m, attached to a leaf of *Laminaria*, on $^3/_7$-1941 (drawn from life on the same day).

Spirorbis granulatus LINNÉ. Northern part of the Sound at fairly great depths, rather rare.

Reproduction: A. Literature. McINTOSH (1923, p. 401) writes: "In this species (March 1st) the ova lie along the intestine — some opposite the stomach, others behind, and thus they differ in position from those of *S. borealis,* which lie chiefly posteriorly and tint the region reddish. In the first week of March the ova are larger than those of *S. borealis,* and, in confinement in the laboratory, they are larger than those fresh from the rocks. On breaking up the tubes of those in confinement in June a number of salmon-colored ova were found toward the smaller end. They were firmly attached by an elongated hyaline process to the inner surface of the tube (Pl. 122, fig. 7e). In each string are about thirty ova arranged for the most part in a double row, and all contained embryos which showed very active ciliary motion at one end like the embryos of *Doris.* A single free cell often accompanied the embryo, which, when liberated, swam by the aid of the cilia. Several free larvae also occurred in the vessel, presenting the usual trochophore outline, viz. an ovoid body and a ciliated ring (prototroch), part of the body in certain positions projecting beyond the ciliated ring. Two eye-specks are present. The posterior bristle or two appear in front of the posterior end, and one or two pairs of the anterior bristles also occur". Besides the embryos inside the tube of the mother animal, young newly settled animals were also found, which shows that the breeding season begins even earlier than March. BORG (1917) describes this species at length from Sweden and figures the operculum both with and without eggs. He states that the brood-protection takes place in the operculum, and he considers this such a well established mode of development that he uses it as a systematic criterion. This is in direct contrast to the observations made by McINTOSH (l. c.).

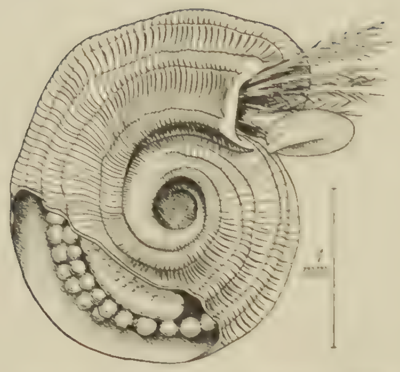


Fig. 80. *Spirorbis granulatus* Linné. **Adult animal. The tube is opened to** show the double chain of eggs lying close to the body of the mother animal. Hittarps reef, depth 10 to 16 m, attached to the shell of a living *Littorina littorea*, on $^{8}/_{7}$-1941 (drawn from life on $^{9}/_{7}$-1941).

B. Own remarks. On $^{8}/_{7}$-41 ten adult specimens were examined, taken on the Hittarp reef, depth 10—16 m, attached to shells of living *Littorina littorea*. They were determined very carefully on the basis of Folke Borg's (l. c.) and Fauvel's (1927) descriptions, and the tubes as well as the animals showed all the characters of *S. granulatus*. The operculum was hollow, and thus seemed well suited for protection of the brood, but it was empty in all the animals examined. However, all the ten specimens found contained eggs and young in the tube (fig. 80). The eggs were yellowish-red and measured 105—110 μ across. A single specimen contained large rotating embryos with red eyes in its tube — a fact which shows that the whole development takes place here. The hatching larvae are smaller than in *S. spirillum*, but of quite the same type, and, like these, will probably swim about in the water for a few hours only. The entirely different modes of brood-protection in this species reported by Folke Borg (from Bohuslän), by McIntosh (near Scotland), and by me from the Sound point to a pronounced lability.

General Discussion of the Polychaetes.

At present bottom stages of 140 species of *Polychaeta* are known from the Sound. To these may be added two species, viz. *Mystides sp.*, and *Poecilochaetus serpens*, known from the Sound in larval stages so old that they may be supposed to metamorphose and settle there. Thus, so far the fauna of the Sound has been found to comprise 142 species. The Spionid-larvae, however, include at least six more species which cannot be referred to any of the adult Spionid-species hitherto known from the Sound, and as there are also other larvae which cannot be referred to any of the adults known from the Sound, it seems likely that future investigations will increase the number of Polychaetes rather considerably. — For 73 out of these 142 species, i. e. 51 per cent, the larval development is known in its broad features, at any rate sufficiently well to show the "ecological type" to which the individual larval species should be referred. These 73 species may be classified as follows (for species marked with an asterisk new data or a discussion of the reproduction or larval occurrence in Danish waters are given in the special part of this paper):

A. Viviparous species: 1 = 1.4 per cent, viz. *Dodecaceria concharum, forma* A (non-pelagic larvae).

B. Species with a non-pelagic development: 20 = 27.4 per cent, viz. **Exogone gemmifera* (brood protection), **E. verugera* (brood protection), **Sphaerosyllis tetralix* (brood protection), **Aphrodite aculeata*, **Pholoë minuta*, **Nereis virens*, *Leptonereis glauca*, **Lumbriconereis fragilis*, **Goniada maculata*, **Aricia cuvieri*, **Scoloplos armiger*, *?*Cirratulus cirratus*, *?*Stylarioides glaucus*, **Arenicola marina* (possibly a short pelagic stage), **Nicomache lumbricalis*, **Ampharete grubei*, *Terebellides stromi*, *Thelepus cincinnatus*, **Fabricia dubia*, and *Dasychone bombyx*.

C. Species with a very short pelagic life (often a few hours to a few days): 10 = 13.7 per cent, viz. **Autolytus prolifer* (brood protection), *Autolytus prismaticus* (brood protection), **Miroserpula inflata* (brood protection), *Filograna implexa* (brood protection), **Pomatoceros triqueter*, *Hydroides norvegica*, ?*Serpula vermicularis* **Spirorbis spirillum* (brood protection), **Spirorbis borealis* (brood protection), and **Spirorbis granulatus* (brood protection).

D. Species with pelagic, lecithotrophic larvae (cf. pp. 436—438): 4 = 6.8 per cent, viz. *?*Mysta barbata*, **Nereis diversicolor*, **Capitella capitata* (brood protection), **Notomastus latericeus* and **Artacama proboscidea*.

E. Species with a long pelagic, planktotrophic larval life (cf. pp. 432—435): 33 = 45.2 per cent, viz. **Harmothoë imbricata* (brood protection), ?*Harmothoë impar* (brood protection), *?*Lepidonotus squamatus*, *?*Gattyana cirrosa*, *Harmothoë sarsi*, *?*Genetyllis lutea*, **Phyllodoce groenlandica*, **Phyllodoce maculata*, ?*Eulalia sanguinea*, **Eulalia* (?*viridis*), **Eteone longa*, **Mystides sp.*, *Tomopteris helgolandica*, **Nephthys ciliata*, **Nephthys coeca*, **Nephthys hombergi*, **Glycera alba*, **Nerine foliosa*, **Polydora ciliata* (brood protection), **Polydora coeca* (brood protection), **Spiophanes bombyx*, *?*Spiophanes krøyeri*, **Magelona papillicornis*, **Poecilochaetus serpens*, *?*Disoma multisetosum*, **Chaetopterus variopedatus*, **Owenia fusiformis*, **Myriochele danielsseni*, **Pectinaria auricoma*, **Pectinaria koreni*, **Pectinaria belgica*, *?*Amphitrite cirrata*, and **Lanice conchilega*.

F. Species which are able to reproduce in a non-pelagic way as well as with planktotrophic, pelagic larvae: 4 = 5.5 per cent, viz. **Nereis pelagica* (pelagic larvae known from the Sound, but the species probably also reproduces in a non-pelagic way here), **Nereis dumerilii* (probably usually non-pelagic in the Sound), **Spio filicornis*, and **Pygospio elegans* (chiefly with pelagic larvae in the Sound).

Thus, when *Pygospio elegans* and *Nereis pelagica* (both known as pelagic larvae from the Sound) are regarded as species with pelagic larvae, it can be stated that 40 out of the 73 species examined, i. e. 55 per cent, have a long pelagic larval life. If we consider the 49 per cent of Polychaete species found in the Sound the larval development of which is unknown, it seems likely, however, that the percentage of species with a long pelagic larval life of the whole Polychaete-fauna in the Sound is somewhat smaller than appears from the above figures. Judging from their egg size, their Arctic distribution, etc., most of the larger systematic groups the development of which is unknown seem to develop in a non-pelagic way (e. g. *Sphærodoridae*, *Chloraemidae*, *Scalibregmidae*, *Maldanidae*, and *Ampharetidae*). But in spite of this there seems also to be a rather large number of these unexamined bottom-forms which have pelagic larvae. The six species of larvae belonging to unknown *Spionidae*, the larva of an unknown Terebellid, and several other larvae seen a few times and hitherto neither figured nor described, point in this direction.

Adult Polychaetes constitute a fairly large percentage of the bottom fauna in the Sound. Within the 300 bottom samples (PETERSEN 1911, Table VI, no. III—VIII) taken throughout the Sound the number of adult Polychaetes which have pelagic larvae seem to constitute about 30 per cent of the number of adult invertebrates with a pelagic development on the level bottom, and a rough estimate seems to show that they will constitute 20–25 per cent if the epifauna is also included. These percentages agree closely with those calculated for the bottom stages of Echinoderms with pelagic larvae (cf. p. 362), but while the adults of these two groups show nearly identical percentages in the Sound, their percentage numbers of larvae in the plankton are strikingly different. The Echinoderm-larvae constitute only 1.9 per cent of all the bottom animal larvae of the main series from Ven and Helsingør, while the Polychaete-larvae constitute 10.9 per cent of the same series, viz. 15.1 per cent off Ven (45 main-series), and 6.0 per cent off Helsingør (20 main-series). The causes of the surprising small number of Echinoderm-larvae are discussed on p. 363. The causes of the larger number of Polychaete-larvae may probably be found in the following facts: The larger amount of eggs shed per female per season; the greater power of resistance to the changing salinity and temperature found in most Polychaete-larvae (thus above all in the dominating *Polydora*-larvae); the hatching of most of the Polychaete-larvae in older stages which have during the earliest stages been protected in the tube of the mother animal, in an egg-capsule, or in an egg-jelly; and, finally, the large ability of locomotion in Polychaete-larvae (in contrast to the nearly passive floating of the Echinoderm-larvae. Cf. further the discussion on pp. 394—396).

Figs. 193 and 194 show the occurrence of Polychaete-larvae in our main-series off Ven and off Helsingor respectively. The table on p. 372 is a supplement to the figures from Ven, and comprises the main-series in the months from August 1936 to August 1937 from which only an estimate, but no exact count, of the larval number is available. — Off Ven (fig. 193) only one constant annual maximum (dominant: *Polydora*-larvae) seems to occur, viz. in March to May. Besides this a sudden extra breeding of *Polydora* may give rise to spontaneous maxima at various times of the year, thus in February and (as shown by pump-series) in August. The larvae decrease in number during the summer to reach their lowest figures from late August to January. — The same spring maximum, though not by far so pronounced as by Ven, is found off Helsingor, here also with *Polydora*-larvae as dominants, decreasing during the summer to reach an absolute minimum in the autumn and early winter.

The common features for the whole Sound are, then: from a spring maximum in March to May with larvae of *Polydora ciliata* and *P. coeca* together with smaller numbers of larval *Harmothoë imbricata, Phyllodoce groenlandica, Eteone longa, Myriochele danielsseni,* and the lecithotrophic larvae of *Nereis diversicolor* and *Artacama proboscidea*, the number of larvae will decrease considerably during June. In July a number of pronounced "summer larvae" will appear with larvae of *Pygospio elegans* (large larvae), *Magelona papillicornis, Disoma multisetosum, Poecilochaetus serpens,* and *Pectinaria koreni* as the most characteristic types. They are all rather few in number and occur together with the laggards from the spring maximum, of which especially *Phyllodoce groenlandica* is normally met with during the whole summer. In the summer a maximum of *Polydora*-larvae, quite unexpected and confusing, may likewise set in. Investigations have shown, however, that the *Polydora*-larvae of the spring maximum are mainly associated with the Baltic surface layer, while the *Polydora* larvae occurring in the summer live at greater depths, i. e. in the Kattegat water. Thus in spring as well as in summer the spawning seems to be correlated with the rising temperatures. — The larvae of the summer plankton will gradually decrease in number during the autumn, and no new larval types will appear until December-January. Then the winter spawning sets in with larvae of *Nephthys ciliata, ?Mysta barbata* (especially in the northernmost part of the Sound), and *Nerine foliosa*, with larvae of *Pygospio elegans* and *Glycera alba* as the less numerous accompanying species. — All these species of larvae have, thus, their main occurrence in the plankton at the time of the year when no production of phytoplankton takes place in the Sound (cf. pp. 433—434), and a closer examination seems to show that precisely these larvae are able to thrive in the plankton under such poor conditions. Thus the larvae of *?Mysta barbata* are lecithotrophic and accordingly independent of the plankton as a source of food; the larva of *Nephthys ciliata* feeds on large specimens of *Coscinodiscus* (the only phytoplankton organisms still of frequent occurrence), and, when these have disappeared, on Lamellibranch larvae (maximum for larvae of *Mya truncata*). AIYAR's (1933) observations from the Madras coast (India) show, further, that larvae of a species of *Glycera* of the same type and size as those found in the Sound are

Larvae of *Errantia*
off Ven . . . . 8.4 %
- Helsingør . . . . 38.2 -
Total . . . 15.8 %

Larvae of *Sedentaria*
off Ven . . . . 83.1 %
- Helsingør . . . . 56.2 -
Total . . . 76.5 %

	Off Ven	Off Helsingør	Total
Polynoidae	0.6 %	5.8 %	1.8 %
Phyllodocidae	5.2 -	8.3 -	5.9 -
Nereidae	1.9 -	8.8 -	3.6 -
Nephthydidae	0.6 -	14.7 -	4.3 -
Glyceridae	0.1 -	0.6 -	0.2 -
Polydora	69.0 %	25.9 %	58.4 %
Other *Spionidae* . . .	8.9 -	21.6 -	12.1 -
Magelonidae	0.3 -	0.6 -	0.3 -
Disomidae	1.8 -	1.5 -	1.7 -
Capitellidae	0.4 -	0.5 -	0.5 -
Oweniidae	0.2 -	0.3 -	0.2 -
Amphictenidae	1.2 -	1.7 -	1.3 -
Terebellidae	1.3 -	4.1 -	2.0 -
Unknown sp.	8.5 -	5.6 -	7.7 -
	100.0 %	100.0 %	100.0 %

also able to feed on large individuals of *Coscinodiscus*. Finally, the pelagic stage of *Pygospio elegans* seems to be rather short and, therefore, less dependent on the food supply in the plankton. — These larvae of winter spawning specimens decrease gradually in number, until the spring maximum suddenly sets in, in March to May (in certain years even earlier).

As a whole, the maxima of Polychaete-larvae in the Sound are not by far so pronounced and so well delimited as for instance those of the Echinoderm-larvae, which have a spring maximum and an autumn maximum with quite different species (cf. p. 364). This is especially due to the fact that all maxima within the Polychaete-larvae are numerically dominated by the same species, viz. the *Polydora*-larvae, which — quite unexpectedly — seem to be able to commence spawning at nearly any time of the year. The larvae of for instance *Harmothoë imbricata*, *Pygospio elegans*, and *Capitella capitata* may also be found in all months of the year, though their numbers may show maxima and minima. The reasons of this are probably to be found in the more extensive vertical distribution of several species of Polychaetes in the Sound, where many of the species occur in the "Baltic water" as well as in the "Kattegat water". A population of such a wide vertical range will at a given date be exposed to quite different hydrographical conditions according to the depths. The part of the population living in Baltic water, for instance, will be exposed to its maximum temperatures in June-July, while the part of the same population living in Kattegat water will be exposed to a corresponding maximum in September-November (cf. pp. 23—25), and the intermediate stock of the population will be exposed to its maximum temperatures within a period intermediate between these two extremes. As, further, the temperature is the most essential spawning-stimulus, it is easily understood that the breeding season for such a population as a whole will be long. — The Echinoderms, however, are nearly exclusively associated with the Kattegat water, i. e. the whole population will be exposed to the same, or nearly the same, temperatures at the same time of the year, and the breeding season will, therefore, be distinctly delimited and short. Studying the graphs on p. 400, it will be seen, that while the number of larval species within the groups Echinoderms, Prosobranchs, and Lamellibranchs vary considerably at the different seasons of the year, Polychaete-larvae of nearly the same number of species seem to occur in every month of the year, a fact which is partially explained in the discussion given above.

The pelagic Polychaete-larvae examined in our main-series during the three years with exact counts, viz. from Ven 15265 (in 45 main-series) and from Helsingør 4324 (in 20 main-series), totalling 19600 larvae, are distributed within the systematic groups as shown in the table on p. 143.

Thus larvae of errant Polychaetes constitute on an average only one-sixth of the number of Polychaete-larvae collected. The dominant larvae of errant species are *Phyllodoce groenlandica*, ?*Mysta barbata*, *Nereis diversicolor*, and *Nephthys ciliata*. Among the larvae of sedentary Polychaetes, the *Spionidae* are absolutely dominant, constituting together 70.5 per cent of all the larvae of Polychaetes known from the Sound. The two species of *Polydora*-larvae mentioned above constitute 58.4 of these 70.5 per cent, and may now and then dominate the whole plankton. This is still more distinct in the Copenhagen harbour, whence Erik Smidt (1944) speaks of "*Polydora*-plankton". Next to dominate within the sedentary forms are the larvae of *Terebellidae*, represented nearly exclusively by one single species, viz. a lecithotrophic larva probably belonging to *Artacama proboscidea*, which within a short period in the spring occurs in rather large numbers in the plankton.

Thus, only a few species of the large number of larvae met with are of quantitative inportance in the Sound, as was also the case with the Echinoderm-larvae. Larvae with a short pelagic life — among others larvae of such common species as *Pomatoceros triqueter* and *Spirorbis borealis* — are only met with in the plankton in a few, scattered specimens without the slightest quantitative importance.

Among the Polychaete-larvae with a long pelagic life it seems possible to distinguish roughly between those belonging to infauna-parents and to epifauna-parents respectively. As infauna-Polychaetes with pelagic larvae in the Sound we regard *Nephthys*, *Glycera*, all *Spionidae* apart from *Polydora ciliata* but including *Polydora coeca*, *Magelona*, *Poecilochaetus*, *Disoma*, *Chaetopterus*, *Capitella*, *Owenia*, *Myriochele*, *Pectinaria*, and *Artacama*. As epifauna-Polychaetes with pelagic larvae we regard: All *Polynoidae*, *Genetyllis*, *Phyllodoce*, *Eteone*, *Nerine*, *Polydora ciliata*, and ?*Amphitrite*.

The quantitative occurrence of larvae belonging to these two groups is as follows:

Ven plankton		Helsingør plankton		Average for both stations	
Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna
15006 larvae	8837 larvae	5558 larvae	1702 larvae	20564 larvae	10539 larvae
= 63.0 %	= 37.0 %	= 76.5 %	= 23.5 %	= 66.0 %	= 34.0 %

Thus two-thirds of the larvae found belong to infauna parents in spite of the fact that two of the infauna-Polychaetes most dominant quantitatively, viz. *Terebellides strømi* and *Scoloplos armiger*, have a non-pelagic development. Further, the one-third of the larvae belonging to epifauna parents is probably estimated two high, as *Polydora ciliata* in the Sound — though normally an epifauna animal — seems to be able to form clay tubes on the level sea-bottom and hence should partially be referred to the infauna.

While all northern Echinoderms with pelagic larvae shed their eggs freely in the water, this is only the case within a minority of the Polychaetes. Such freely shed eggs are known from: *Nephthys, Nerine, Chaetopterus, Pectinaria,* and *Amphitrite* (and among species with a non-pelagic development from *Arenicola, Ampharete, Amphicteis, Thelepus,* and *Nicolea venustula*). Several genera shed their eggs imbedded in a gelatinous jelly, thus nearly all *Phyllodocidae,* some *Maldanidae,* and *Owenia* (and among those with a non-pelagic development *Scoloplos* and *Terebellides*). Other forms, e. g. *Spio filicornis,* lay their eggs in free capsules adhering to a substratum. Finally, a large number of species have a more or less pronounced brood protection. This brood protection is most primitive in forms which shed their eggs imbedded in slime or in primitive capsules inside the tube of the mother animal; this is known from: *Polydora, Pygospio,* certain species of *Nereis, Capitella,* and several species of Serpulids, e. g. *Filograna,* and *Spirorbis,* the last two genera with a shortened pelagic life. Another primitive form of brood protection is that the eggs, imbedded in slime, are deposited under the elythra or the dorsal cirri of the mother animal, known in all species of *Harmothoë* examined and in *Notophyllum.* In the Serpulid genus *Miroserpula,* the larval development of which closely resembles that of *Spirorbis,* the young embryos are protected in special brood chambers outside the calcareous tube of the mother animal. Finally, in a few species, the brood protection has reached a high degree of organisation, e. g. in the genus *Autolytus,* where the young develop in a sac on the ventral side of the mother animal (shortened pelagic life), and in the genera *Exogone* and *Sphaerosyllis,* in which the eggs and embryos develop attached to the parapodial cirri of the mother (non-pelagic larvae). In *Dodecaceria concharum* (form *A*), finally, viviparity is a normal mode of development.

As will be seen from the above, most of the Polychaete-larvae in the Sound will only appear in the plankton in later stages of their embryonic development. Some of them appear in the *Trochophora* stage, several in the *Metatrochophora*-stage I or II, i. e., in stages which are — in most cases — able to feed on the plankton immediately after they have been hatched, while e. g. the Echinoderm larvae spend several days floating passively in the plankton during the first cleaving stages, taking no food from the plankton during this period.

The duration of the pelagic life is discussed at length on pp. 451—457. From this discussion it seems to appear that the Polychaete larvae from northern seas, which are reared in nature or under laboratory conditions resembling natural conditions as closely as possible, will take on an average two to four weeks to pass from fertilisation to metamorphosis when spawned in the warm season. Examples are: *Eulalia viridis* (10—13 days), *Nereis pelagica* (18 days), *Scolecolepis fuliginosa* (35 days), *Polydora ciliata* (at least 6 weeks), *Owenia fusiformis* (27 days), and the lecithotrophic *Capitella capitata* (7—9 days). This seems to be in good agreement with the time used by other pelagic larvae of invertebrates within the same season.

The larva of *Magelona papillicornis* will normally feed exclusively on animal food (Lamellibranch larvae and larvae of Polychaetes), and the larvae of *Chaetopterus, Nephthys,* and *Polydora* may feed on other planktonic animals. The two last-mentioned genera seem always to feed on Lamellibranch larvae when the quantity of phytoplankton is poor. In such seasons they must be regarded as very significant competitors, which may devour and decimate a whole stock of Lamellibranch larvae, and in this way they may considerably influence the recruiting of young fish-food-animals on the bottom.

Young herrings may eat Polychaete larvae, and the same is the case with Actinians, with several Ctenophores and Medusæ, and with Amphipods and Cumaceans (cf. pp. 467—471). *Magelona papillicornis* may also feed on other worm larvae. Polychaete larvae, however, seem to be of little value as food for other animals, and the "waste" percentage of larvae during the pelagic development which can be ascribed to enemies seems to be rather small. This is partially explained by the fact that the Spionid-larvae, which dominate in the northern seas, are able — when irritated or in danger — to erect their long provisional larval bristles like an angry hedge-hog. When pipetted up from a Petri-dish, such Spionid-larvae are able to resist the sucking of a rather wide pipette, and only a rather vigorous enemy with a very wide mouth will be able to swallow even small specimens of larval Spionids.

Summary of Discussion.

One hundred and forty-two species of Polychaetes are known from the Sound as adults, larvae, or both. The larval development is known for 73 of them: one is viviparous with non-pelagic larvae, 20 have a non-pelagic development, 10 have a very short pelagic life, 5 have pelagic lecithotrophic larvae, 33 have a long pelagic, planktotrophic larval life, and 4 may reproduce either with pelagic larvae or with a non-pelagic development. Thus, 40 or 41 species — about 55 per cent — have a long pelagic larval life. In the bottom stage the Polychaetes constitute about 30 per cent of all the invertebrate specimens with pelagic larvae in the infauna and a total of about 20–25 per cent if the epifauna is included, while the larvae of these two groups represent 10.9 per cent of all the invertebrate larvae in the Sound plankton. The Polychaete larvae hatch normally in older stages able to feed immediately on the plankton. Their resistance to changing salinity and temperatures is fairly great, and the individual females will generally spawn a large number of eggs per season. — The larval seasons are as follows: a spring maximum with larvae of *Polydora ciliata* and *P. coeca* (and *Harmothoë, Phyllodoce, Eteone, Myriochele, Nereis diversicolor*, and *Artacama*) decreasing during June, and supplemented in July with "summer-larvae", i. e. *Pygospio, Magelona, Disoma, Poecilochaetus,* and *Pectinaria* — and sometimes with a spontaneous maximum of *Polydora*. The larval number will now decrease, until the winter spawning in December-January sets in with larvae of *Nephthys, ?Mysta,* and *Nerine* as dominants. These larvae decrease gradually in number, until — in March — the spring maximum sets in. Several species of larvae may occur in every month throughout the year. This is especially due to species the adults of which have a wide vertical range within the Sound, and which, therefore, will spawn at different times in the Baltic water and in the Kattegat water, according to the temperature maxima of these layers. — Larvae of errant Polychaetes constitute 15.8 % and those of sedentary Polychaetes 76.5 % in the Sound plankton (plus 7.7 % indeterminable larvae). Spionid-larvae constitute 70.5 % of all the larval Polychaetes from the Sound. The *Polydora*-larvae alone constitute 58.4 % of these 70.5 %. Larvae with a short pelagic life are quantitatively of no significance in the plankton. — Larvae belonging to "infauna parents" comprise 66 %, or probably more, of all the Polychaete larvae found in our main series. Northern pelagic Polychaete larvae will on an average take 2—4 weeks to pass from hatching to metamorphosis in the warm season. The species able to feed on larval Lamellibranchs may give rise to a considerable "waste" of these during certain seasons. — The larvae seem only to be of little importance as food for other animals.

3. Nemertini.

During our investigations the Nemertines have not been studied in such great detail as other groups of invertebrates. The difficulty in identifying most of these species requires a special technique and a thorough treatment focussed only on the group in question, and up to the present we have had no time to spare for this purpose. However, CHR. OVERGAARD, m. sc. from the laboratory at Helsingor, has commenced a detailed investigation of this group, and his observations on the Nemerteans from the Sound, their breeding biology and larval development, will be continued and the results published during the following years. — The present remarks should, therefore, only be regarded as preliminary notes based partially upon information supplied by Mr. OVERGAARD.

So far 18 species of Nemertines are known from the Sound. The species marked with an asterisk are recorded from the Sound for the first time thanks to OVERGAARD's investigations:

Palaeonemertines: Four species, viz. **Tubulanus superbus*, *Cephalothrix linearis*, *Cephalothrix rufifrons*, and **Procephalothrix* (*filiformis*?).
Heteronemertines: Five species, viz. *Lineus ruber*, **Lineus* (*lacteus*?), **Micrura purpurea*, **Micrura fasciolata*, and *Cerebratulus marginatus*.
Hoplonemertines: Eight species, viz. *Oerstedia dorsalis*, **Emplectonema sp.*, **Prostoma melanocephalum*, **Prostoma obscurum*, **Prostoma flavidum*, **Prostoma candidum*, **Amphiporus lactifloreus*, and *Amphiporus pulcher*.
Bdellonemertines: One species, viz. *Malacobdella grossa*.

OVERGAARD's investigations have increased the number of Nemertine species known from the Sound by 200 per cent, and OVERGAARD mentions eight further species from the Sound, which are still undetermined but will be described later.

It is a well known fact that the development of the Nemertines may take place in three embryologically different ways, viz. by:

1. A direct development, in which the embryo develops into the young bottom stage without any metamorphosis.
2. DESOR's larvae, developing within a membraneous, ciliated larval epithelium, from which they will not hatch until they have almost reached the type of the adults. (Only known from *Lineus ruber*).
3. The Pilidium larvae, — a characteristic pelagic stage, through which the young bottom stage is reached after a metamorphosis.

From an ecological point of view, however, the modes of development must be divided in quite a different way, viz. into

1. Species with a non-pelagic development.
2. Species, which have a pelagic stage but are lecithotrophic, i. e. take no food from the plankton.
3. Species with a pelagic, planktotrophic life, i. e. the *Pilidium*.

As is well known, *Pilidium* larvae seem only to occur within the Heteronemertines, while the Palaeonemertines, Hoplonemertines, and Bdellonemertines all have a direct development, but as this direct development may, or may not, have a pelagic phase, it seems reasonable to consider the individual species from the Sound and ascertain their "ecological type" of larval development.

Palaeonemertines.

Tubulanus superbus KÖLL.: JOUBIN (1890), observed spawning specimens and states that the development was carried through "parfaitément", but as he gives no further remarkable details of the development, it seems justifiable to conclude that it is roughly parallel to that known for other Palaeonemertines, i. e. direct as in the related *Tubulanus pellucidus* (Coe 1943). Hence it is unknown whether a pelagic phase is present or not. — When irritated, ripe females spawned apparently ripe eggs in the Sound.

Cephalothrix linearis Rathke: McIntosh (1873), Barrois (1877), Coe (1899 a, p. 235), Dawydoff (1928), and Smith (1935) describe the development of this species, viz. direct, but with a pelagic swimming stage in which the oesophagus has not yet formed. The larva is accordingly pelagic, lecithotrophic. — Natural spawning has been observed in the Sound.

Cephalothrix rufifrons Johnston: Smith (1935) gives an account of the development, which is direct with a pelagic phase of at least two weeks. The young pelagic larvae are positively phototactic, while older pelagic larvae are indifferent to the light. They take no food from the plankton, — that is to say they are lecithotrophic. — Natural spawning has been observed in the Sound.

Procephalothrix (filiformis?): Larval development unknown. — For the North American *Procephalothrix spiralis* Coe (1943, p. 232) observed that during the warmer months of the year the eggs are deposited by night in a string of mucus. The larvae, though having a direct development, swim and feed on protozoans.

Heteronemertines.

Lineus ruber O. F. Müller: Desor (1850), Hubrecht (1885 a, 1885 b), Barrois (1877), Arnold (1898), Nussbaum & Oxner (1913), G. A. Schmidt (1932, 1934) and Coe (1943, p. 243) have studied the reproduction and development. When ripe a male and a female worm place their bodies side by side and exude about themselves a thick sheat of highly viscous mucus. Here the eggs are extruded and fertilized, and the parent animals leave the mucus in which the eggs develop. Two types of eggs and development are known, viz. 1) the Desor-type: The embryos develop within the ciliated larval epithelium (within the egg-mass) and will not hatch until reaching the crawling stage, in which they are roughly of the same type as the adults. From an ecological point of view the term "Desor's larva" should be replaced by "Desor's embryo", as there is no free larval stage. 2) The nurse-egg-type: The embryos hatch as large young in the crawling stage. — Natural spawning known from the Sound.

Lineus lacteus Rathke: Metschnikoff (1870, 1882) has studied the reproduction and larvae, the latter being pelagic already from the gastrula stage, developing into typical *Pilidium*-larvae (good figures).

Micrura fasciolata Ehrenberg: Joh. Müller (1847, 1854), Coe (1899 a, p. 236), and G. A. Schmidt (1937, pp. 446—447) discuss the typical *Pilidium* larvae, probably identical with *Pilidium gyrans* Joh. Müller. Coe (1943) figures the Pilidium larvae of the North American species *Micrura coeca* (p. 208), and *M. leidyi* (p. 251).

Micrura purpurea Dalyell: Unknown, but *Pilidium* larvae seem to be typical of all species of the genus *Micrura* hitherto examined.

Cerebratulus marginatus Renier: Coe (1899 a, 1943) and Schmidt (1937, pp. 446) describe the reproduction and figure the larvae, which reached the free-swimming *Pilidium* stage two days after fertilisation. One day later the first signs of a metamorphosis were seen, but pelagic larvae occurred in aquaria as late as 18 days after fertilisation. — Natural spawning has been observed in the Sound.

Hoplonemertines.

Oerstedia dorsalis Abildg.: Coe (1943, p. 269 and fig. 40) describes the reproduction and figures the larvae. A few large eggs per female are shed during the summer. Development of the direct type. The larvae take no food from the plankton and their planktonic life seems to be short. — No observations from the Sound.

Emplectonema sp.: Reproduction unknown.

Prostoma melanocephalum Johnston: Reproduction unknown. — Natural spawning observed in the Sound.

Prostoma obscurum Schultze: Schultze (1851) mentions the viviparity of this species. The young hatch in the crawling stage, when they are very like the adults in shape. — Viviparity was also observed in specimens from the Sound. — Coe (1943, p. 298—300) describes and figures the development of the fresh-water species *Prostoma rubrum* from N. America; eggs 30—60 in number, are laid in a tenacious mucus and develop into free-swimming larvae without metamorphosis.

Prostoma flavidum Ehrenberg: Reproduction unknown.

Prostoma candidum O. F. Müller: Reproduction unknown.

Amphiporus lactifloreus Johnston: McIntosh (1873) and Barrois (1877) describe the direct, non-pelagic development of this species. The eggs are about 350 μ in diameter (McIntosh l. c.), and the young hatch in the crawling stage; they are then very like the adults. — Natural spawning has been observed in the Sound.

Amphiporus pulcher Johnston: Unknown in the literature. — Natural spawning observed in the Sound. The ripe eggs are about 400 μ across, i. e. larger than those of *Amphiporus lactifloreus* (about 350 μ). As this latter species is known to reproduce in a non-pelagic way, it can be taken for granted that the pelagic larval stage is reduced also in *Amphiporus pulcher* with its still larger eggs. -Coe (1943) describes the reproduction in the N. American species *Amphiporus (Zygonemertes) virescens* (free-swimming, lecithotrophic larvae without metamorphosis), *Amphiporus cruentatus* and *A. ochraceus* (both with a direct development).

Bdellonemertines.

Malacobdella grossa O. F. Müller: Gering (1910) and Hammarsten (1918) have described the development, which is direct. The larvae have, however, a pelagic phase, swimming at first near the surface, later on near the bottom. They take no food from the plankton, i. e. they are lecithotrophic.

Thus according to our present knowledge:

A direct, non-pelagic development is known in *Lineus ruber, Prostoma obscurum, Amphiporus lactifloreus,* and *Amphiporus pulcher,* and is probably also the usual mode of development in other Hoplonemertines.

A direct development, with pelagic, lecithotrophic larvae is known for *Cephalothrix linearis, Cephalothrix rufifrons,* and *Malacobdella grossa*, and probably also occurs in other Palaeonemertines.

An indirect development with pelagic planktotrophic larvae of the *Pilidium* type is known for *Lineus lacteus, Micrura fasciolata,* and *Cerebratulus marginatus,* and probably also occurs in *Micrura purpurea*, in two other species of *Lineus*, and two other species of *Cerebratulus* found in the Sound and referred by Overgaard to genera but not to species.

Nemertine larvae with a direct development leading to pelagic lecithotrophic larvae have not been observed in our main series, but tiny and little characteristic as they are, small numbers of them may have been confused with larvae of for instance Actinians or with other small planula-like types. The literature seems to show that their pelagic phase is of very short duration. If so, they are of little importance in the plankton (cf. the larvae of the Prosobranch *Hydrobia ulvae*, p. 185), and our main series show that they must be sparsely represented in the actual samples.

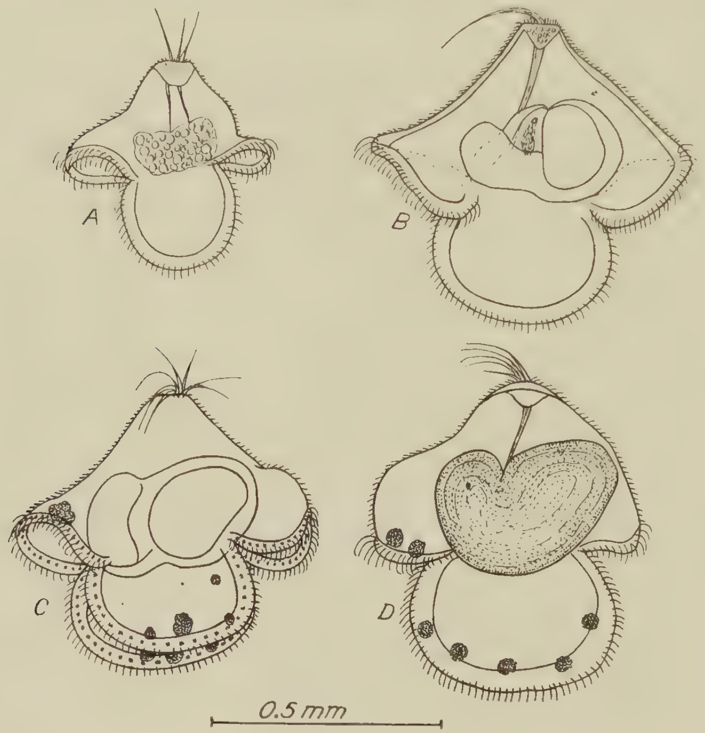


Fig. 81 A-D. *Pilidium*-larvae from plankton off Ven, depth 18—0 m, drawn from life on the day of capture. — *A.* and *B.* Smaller (A) and larger (B) larvae af the *Pilidium-magnum*-type ("*Pilidium* type A", see the text p. 150), taken on $^{27}/_{9}$-1936. — *C.* and *D.* Larvae of the *Pilidium-conussoidale*-type ("*Pilidium* type B", see the text pp. 150—151). — *C.* Large larva with large yellow spots and small yellowish brown dots along the margin (caught on $^{31}/_{10}$-1936). — D. Older larva of the same species with the young Nemertine formed inside (caught on $^{27}/_{9}$-1936).

Pilidium larvae, however, occur in our main series, but in such small numbers that they only constitute about 0.01 per cent of all the bottom animal larvae counted. They may be divided into three distinct types, two of them are typical autumn-larvae, while the third occurs in the spring.

Pilidium type A (cf. fig. 81 A—B): Quite colourless, with equally large anterior and posterior lobes and with broad, symmetrically shaped and placed lateral lobes. The size of one of our large larvae (fig. 81 B), from the base of the apical tuft to the distal end of a lateral lobe, is 670 μ. The larva in question shows close points of similarity to the *Pilidium magnum* type (cf. G. A. Schmidt, 1937, p. 445), the largest larvae of which measure up to 800 μ. Unfortunately the identity of the *Pilidium magnum* type is still unknown, but it seems to belong to a genus which has a tail in the adult stage. Larvae of type A are present in our samples taken off Ven on: $^{26-27}/_{9}$-36 (several spms.); $^{17}/_{10}$-36 (1 spm.); $^{1}/_{11}$-36 (1 spm.); $^{9}/_{10}$-37 (3 spms.); $^{18}/_{12}$-37 (1 spm.); $^{6}/_{1}$-38 (1 large spm.); $^{19-20}/_{8}$-38 (several spms.); $^{8}/_{10}$-38 (1 spm.), and off Helsingør on: $^{7}/_{10}$-41 (1 spm.), and $^{25}/_{10}$-41 (2 spms.); thus they occur from late August to early January. This seems to indicate that they are derived from parents living at greater depths, i. e. in the Kattegat water.

Pilidium type B (cf. fig. 81 C—D): Characteristic large yellow spots occur along the margins, which are further bordered by minute yellowish-brown dots. The anterior lobe seems to be somewhat smaller than the posterior, with a faint asymmetry in the position of the lateral lobes. The apical tuft is extremely short. Verrill (1892, p. 39, fig. 6) figures a *Pilidium* from

New England, which, apart from the length of the apical cilia, agrees well with our type B from the Sound. The size is the same: From the apical tuft to the distal end of the lateral lobe our larva measures 560—640 μ, Verrill's larvae are 590 μ, and they have both the same yellow spots along the margin. Verrill seems to be inclined to refer his larvae to a species of *Micrura*, but admits that it may belong to *Cerebratulus*. Coe (1943, p. 254) refigures Verrill's larva as the larva of *Cerebratulus lacteus* which species according to Friedrich (1936) seems to be absent from our seas. — It seems most likely, however, that our larvae belong to the *Pilidium conussoidale* type (cf. G. A. Schmidt 1937, p. 445), which according to the same author seems to belong to the genus *Cerebratulus*. This is further supported by Overgaard's observation, viz. that *Cerebratulus marginatus* is ripe in the late summer and autumn, and the fact that the larvae occur in autumn plankton. — The larva of *Cerebratulus marginatus* described by Coe (1943, p. 257) shows, however, features much different from those of our "Pilidium type B" from the Sound, but this may probably be explained by their different ages, the larva of Coe probably being much younger than our stages. —Larvae

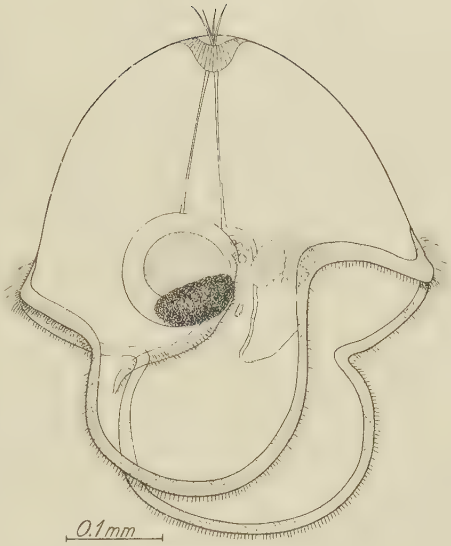


Fig. 82. Nemertine larva of the *Pilidium-magnum*-type (cf. Schmidt 1937). From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40—0 m, caught and drawn from life on $^{18}/_{8}$-1945. The larva is characterised by its colourless, bell-shaped umbrella, its short apical cilia, and the symmetrical position of the lateral lobes.

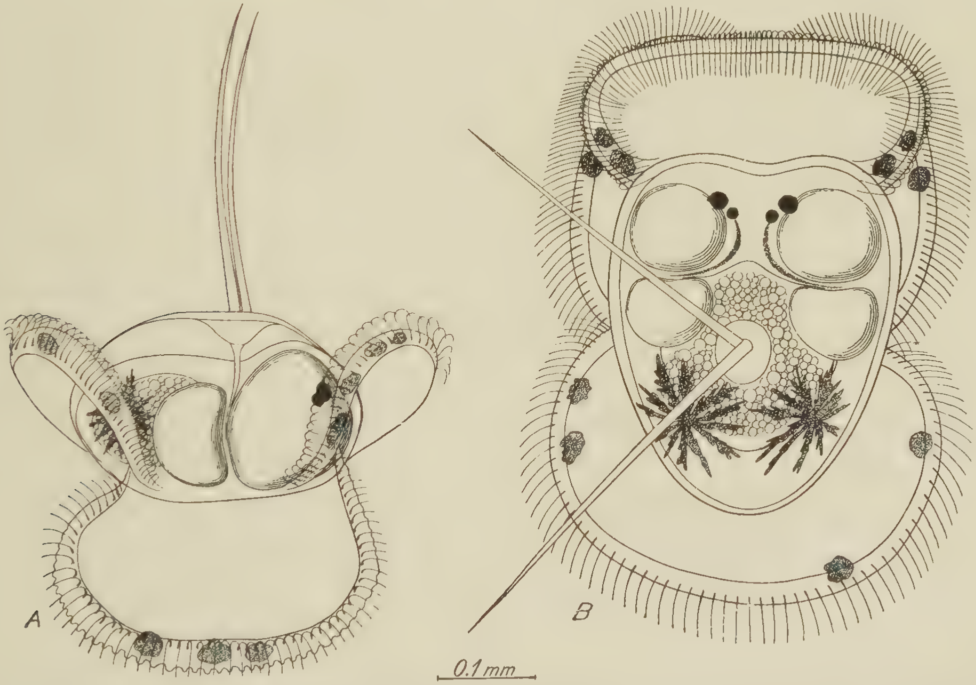


Fig. 83 A-B. Nemertine larvae belonging to the *Pilidium-gyrans*-type (cf. Schmidt 1937). From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40—0 m, caught and drawn from life on $^{16}/_{8}$-1945. In both larvae the young Nemertine is distinctly seen within the umbrella. — *A*. Seen from the right side. — *B*. Seen from the apical side.

of type B are present in our samples taken off Ven on: $^{26-27}/_{9}$-36 (several spms.); $^{7}/_{10}$-36 (1 spm.); $^{1}/_{11}$-36 (1 spm.), and $^{9}/_{10}$-37 (1 spm.), thus occurring from September to November.

Pilidium type C (unfortunately no drawings are available): The larvae are large and have a reddish-brown border of pigment along the margins but no large yellow spots. They are found in our plankton taken off Ven on: $^{23}/_{5}$-37 (1 spm.); $^{18}/_{4}$-38 (5 spms.); $^{10}/_{4}$-39 (3 large spms.), and $^{17}/_{5}$-39 (2 large spms.), thus occurring in the spring (April-May). The larvae occurring at this time of the year — according to our experience — most likely originate from parents living at smaller depths, i. e. in Baltic water.

In August 1945 I had the possibility to study and sketch some *Pilidium* larvae from Gullmarfjord-plankton (Bohuslän, Swedish W. coast). One of them (fig. 82) was colourless apart from yellowish-brown, olive-green, and dark-green areas in the stomach, with a bell-shaped umbrella, and measured 515 μ from the base of the very short apical tuft to the distal end of the lateral lobe. The nearly total symmetry on both sides of a line from the apex to the end of the lateral lobe refers the larva in question to the *Pilidium-magnum* type (Schmidt, l. c., p. 438) although it seems to be different from the "*Pilidium* type A" from the Sound also referred to this type. The *Pilidium-magnum* type thus seems to comprise at least two different species of larvae. — The larvae fig. 83 A-B with their short, elevated anterior and posterior lobes, their large, rounded lateral lobes, and their extremely long apical cilia agree closely with the *Pilidium-gyrans* type as figured by Schmidt (1937, p. 440, Abb. 7c), the closer identity of which is unknown. The border of the lobes was faintly reddish-brown, and the two branched chromatophores and the pigment spots along the margin are yellowish-white in direct light (dark in transmitted light). There are two pairs of eyes. This larva also shows similarities to the larva of Verrill (1892, fig. 6) referred by Coe (1943, p. 254) to *Cerebratulus lacteus*. — The larva fig. 84 may be identical with our "*Pilidium* type C" from the Sound. The ciliary tuft is rather large, the anterior lobe much smaller than the posterior, and the lobes are bordered with small spots which are yellowish-white in direct light, reddish-brown in transmitted light. It seems to belong to the *Pilidium-conussoidale* type to which also our "*Pilidium* type B" seems to belong. *P. conussoidale* is already known to comprise at least two species of *Cerebratulus* larvae (Schmidt 1937, p. 446).

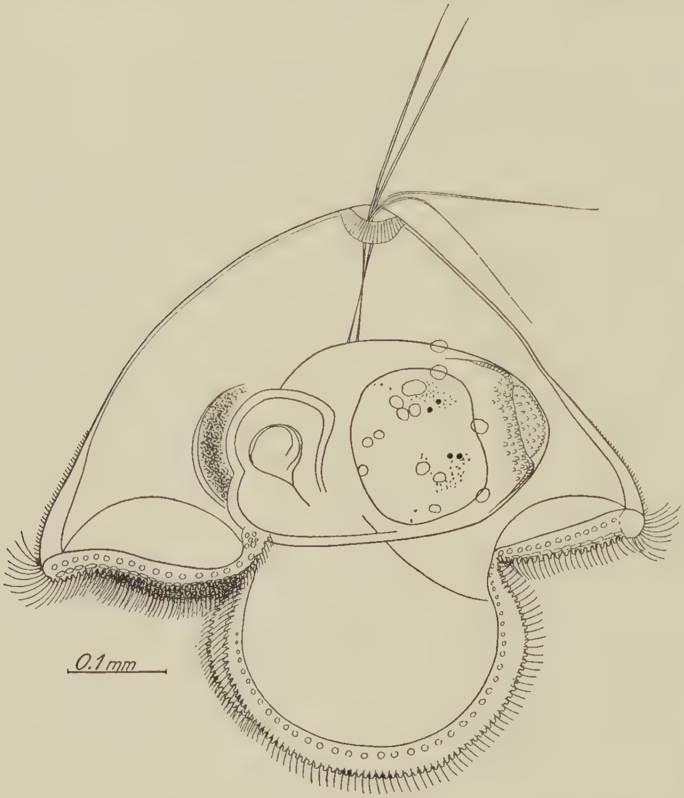


Fig. 84. Nemertine larva of the *Pilidium-conussoidale-type* (cf. Schmidt 1937). From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30—0 m, caught and drawn from life on $^{19}/_{8}$-1945. Seen from the right side with the young Nemertine inside the umbrella. The borders of the lobes have small spots of pigment which are lemon-coloured in direct light, reddish-brown in transmitted light. The stomach has a dark-brown area. The young Nemertine inside is yellowish-white with yellowish-brown pigment spots and four small black eyes.

The paper of G. A. Schmidt (1937) shows the difficulties, but also the possibilities of identifying different species of *Pilidium* larvae met with in the plankton. His fourth main type, viz. *Pilidium auriculatum*, is still unknown from the Sound. — The requirement of food of *Pilidium* larvae seems to be considerable. "Das Bedürfnis nach Ernährung entsteht bei Pilidien sehr schnell" (Schmidt, 1937, p. 426, on larvae of *Cerebratulus*), and our experience from the Sound has shown that *Pilidium* larvae are very sensitive to changes in salinity and temperature.

4. Phoronidea.

Only two species of adult Phoronids are known to occur in the Sound, viz. *Phoronis ovalis* Wright and *Phoronis mülleri* de Selys Longchamps. The first-mentioned species was recorded from the Sound by Brattström (1943), who also mentions the young bottom stages of *Phoronis mülleri* found by the present author in bottle-collectors off Ven in 1939. These two species have thus been overlooked in the Sound up to the most recent years, and it is quite possible, therefore, that still more species of *Phoronis* may occur in the Sound, thus for instance *Phoronis hippocrepia* Wright, known from Bohuslän, and *Phoronis gracilis* van Beneden, known from Heligoland.

The adult *Phoronis mülleri* was described as late as 1904 (from Heligoland, cf. de Selys Longchamp 1904), and it was shown that this species was the parent of the larva described under the name of *Actinotrocha branchiata* Joh. Müller. Apart from their occurrence near Heligoland, the adults of *Phoronis mülleri* were not recorded from northern seas until Gustafson (1936) found them to be extremely common near Bohuslän. The larva, however, *Actinotrocha branchiata*, is commonly met with in plankton from Bergen, St. Andrews, Millport, Bohuslän, the Kattegat, the Sound, and Kiel (cf. Cori 1932). In the paper of Søren Jensen, Johansen, and Levinsen (1903, p. 284) this larva is mentioned from Læsø Rende and Anholt Knob taken in the year 1900, and in the same paper it is stated that it has been observed on several occasions in summer plankton near Frederikshavn, in the Limfjord, and off Hellebæk.

Excellent descriptions and figures of all stages of larvae of *Phoronis mülleri* are given by de Selys Longchamp (1904). His main results may be summarised as follows: Breeding near Heligoland in June to November with a maximum in August. The parents are hermaphroditic. It is unknown whether or not self-fertilisation takes place. The eggs, 50 μ in diameter, are shed freely in the water. Young larvae swim near the surface, older larvae near the bottom. The late larva has 28 larval and 24 definitive tentacles. It feeds on Peridinians, not on Diatoms (Lebour, 1922, p. 649). By the aid of the good and detailed figures larvae in all stages are easily recognisable in the plankton and they provide the final proof of the identity of *Actinotrocha branchiata* with *Phoronis mülleri*. – All *Phoronis* larvae examined from the Sound (fig. 85 A—C) belong to this species. Larvae are present in our main series taken off Ven on: $^{26-27}/_{9}$-36 (a few young and old larvae); $^{17}/_{10}$-36 (a few spms.); $^{1}/_{11}$-36 (2 large spms.); $^{14}/_{11}$-37 (1 young spm.); $^{17}/_{7}$-38 (1 large spm.); $^{11}/_{9}$-38 (8 spms.); $^{24}/_{9}$-38 (1 spm.); $^{8}/_{10}$-38 (one half-grown spm.); $^{25}/_{3}$-39 (1 very young spm.); $^{15}/_{7}$-39 (1 half-grown spm.), and $^{18}/_{8}$-39 (1 young spm.), and off Helsingør on: $^{7}/_{10}$-41 (2 young and 1 large spms.); $^{11}/_{11}$-41 (2 young spms.), and $^{5}/_{9}$-42 (1 young spm.). Thus the season of occurrence is from the middle of July to the middle of November with a maximum in September-October. Quite young larvae (according to de Selys Longchamp 1904 hardly more than 4 days old) as well as late larvae near the stage of metamorphosis may be found.

In August 1945 larvae of *Ph. mülleri* in all stages occurred frequently in the plankton of Gullmarfjord (Bohuslän, Swedish W. coast), and here I sketched two larvae (fig. 85 G—H) considerably larger than those sketched from the Sound (fig. 85 A—C). The largest larva (fig. 85 H, 1400 μ) was larger than the young bottom stages from the Sound (about 900—1000 μ, fig. 85 D—E, see below), a fact which seems to show that this species is able to metamorphose at different sizes. — In the larva fig. 85 H the definitive tentacles have appeared. The orange pigment round the base of the tentacles is present, a brown pigment-lump is seen where the oesophagus merges into the intestine (excretory organ?), and there are yellow spots of pigment on the umbrella and near the anal ciliary ring.

A bottle-collector exposed off Ven at a depth of 16 m from $^{7}/_{7}$-39 to $^{23}/_{8}$-39 contained a young, just metamorphosed bottom stage of *Phoronis mülleri* (fig. 85 D—E). All the tentacles had already developed, most of them were provided with yellow lines of pigment. The body was still roundish to conical, not vermiform as in the adults. Inside the tentacular crown there were two orange-red areas. The area round the tentacles was of an orange colour, with a reddish pigmentation and yellowish lines of pigment. The stomach was yellowish-green. The short tentacles in front show clearly that the young stage belongs to *Phoronis mülleri*. Young in this stage inhabit thin, transparent slime-tubes and are able to move within these tubes. The body showed constant contractions, thus having alternately a spherical or a conical shape.

The same bottle-collector contained a somewhat older, but still young specimen, which showed all the characteristics of the adults (fig. 85 F). The length of the animal was about 3 mm, it inhabited a thin slime-tube with a few grains of sand adhering to it, and had about 38 tentacles. The orange-red areas inside the tentacular crown were distinct as in the younger specimen described above. Young of this type are developed within 6 weeks at most after the settling of the larvae.

The larva of *Phoronis ovalis* seems still to be unknown. HARMER's (1917) suggestion, that *Actinotrocha pallida* belongs to this species, according to DE SELYS LONGCHAMP (1904) and BRATTSTRÖM (1943) seems not to hold good. The species may reproduce asexually by division (HARMER l. c.), but besides this a sexual reproduction may take place. Larvae which may be referred to this species have, however, not been observed in the Sound.

5. Bryozoa.

As was the case in the Actinians, Nudibranchs, Nemerteans, and Crustaceans, the Bryozoans were only roughly treated in our investigation. A detailed investigation of larvae belonging to this group will be published later by Mr. FRITZ JENSENIUS MADSEN. — MARCUS (1940), in

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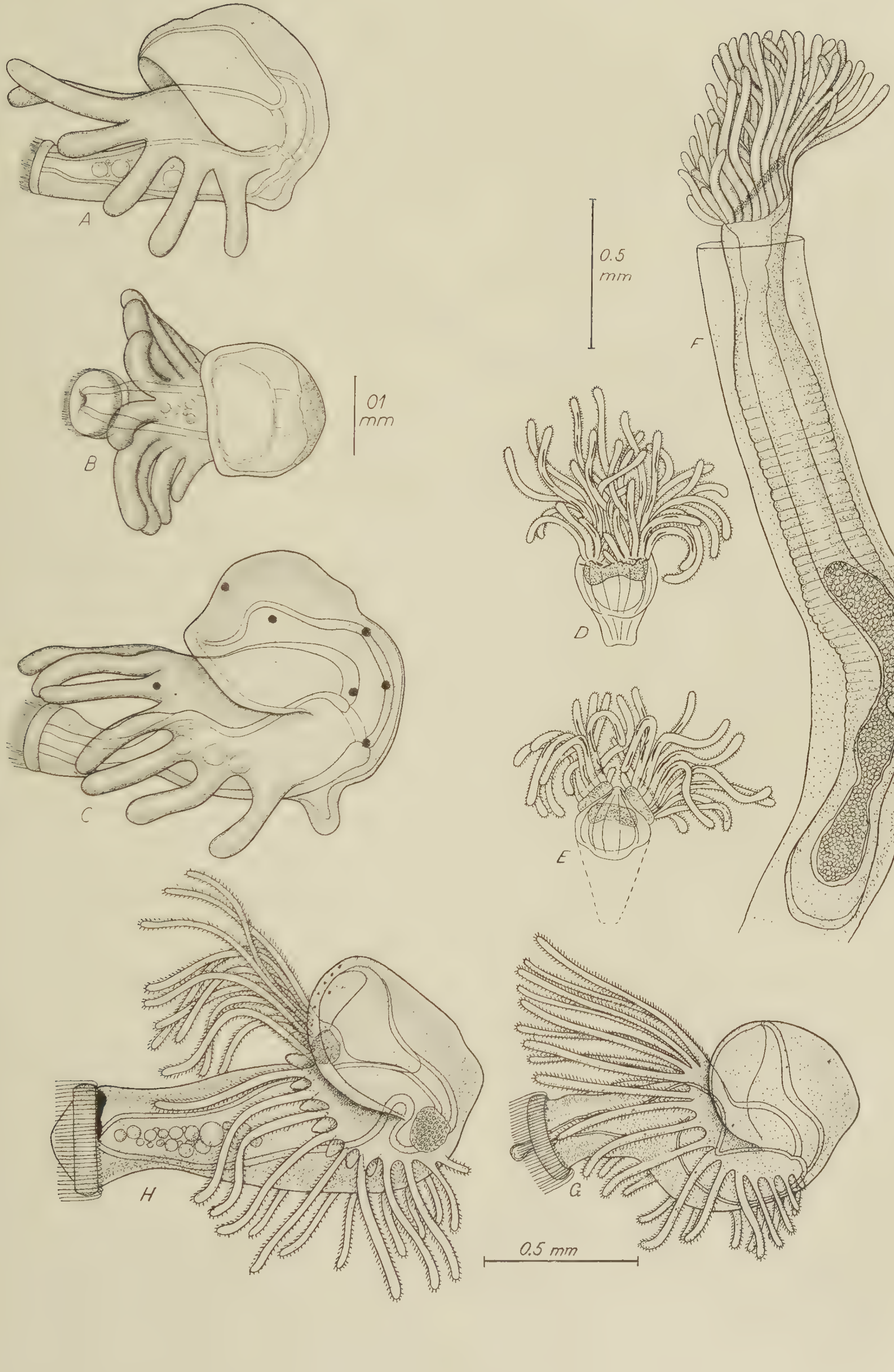
Fig. 85 A-H (see the next page). *Phoronis mülleri* DE SELYS LONGCHAMPS.—*A.* to *C.* Larvae from plankton off Ven, depth 18—0 m, caught and drawn from life on $^{12}/_{8}$-1944.—*A.* and *B.* Larvae of medium size with five pairs of tentacles, seen from the left side (A) and from the dorsal side (B).—*C.* Older larva with six pairs af tentacles and with yellowish-white pigment-spots, seen from the left side.—*D.* to *F.* Young bottom-stages from a bottle-collector exposed off Ven, at a depth of 16 m, from $^{7}/_{7}$ to $^{23}/_{8}$-1939. Drawn from life on $^{24}/_{8}$.—*D.* and *E.* Young bottom-stage just after metamorphosis, without tube and still able to change the shape of its body. Seen from the ventral side (D) and the dorsal side (E, the body may be dilated to the stipled line).—*F.* Bottom-stage in its slime tube 6 weeks at the most after metamorphosis; seen from the left side.—*G.* and *H.* Old larvae from Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40-0 m, caught and drawn from life on $^{16}/_{8}$-1945. The larva fig. 85 H is the oldest planktonic stage found.


A
B
01
mm
C
0.5
mm
D
E
F
H
G
0.5 mm

"Danmarks Fauna", has taken a survey of all Danish *Bryozoa*, also those found in the Sound. In this fine paper, in which all earlier literature is considered, he seems, however, to have overlooked the papers of Lönnberg (1898, 1899), which mention e. g. *Loxosoma phascolosomatum* and *Tubulipora flabellaris* from the Sound.

Entoprocta (= *Kamptozoa*).

The only species recorded from the Sound is *Loxosoma phascolosomatum* (Lönnberg 1898, p. 44), which occurs rather commonly attached to *Phascolion strombi*. Further, according to Marcus (1940), *Barentsia gracilis* and *Pedicellina cernua* are known from the Kattegat as well as from the Baltic, the latter for instance from Skelderviken just N. of the Sound (Lönnberg 1903, p. 57), and accordingly it probably lives in the Sound also. Larvae of these three species may, therefore, occur in our plankton. Larvae of *Entoprocta*, however, swim and crawl for a very short time only before settling (Marcus l. c., p. 10), and accordingly their importance in the plankton seems to be small (cf. similar conditions in the Prosobranch *Hydrobia ulvae* p. 185). Barrois (1877 a), in a very beautiful paper, and Cori (1930) have figured the larvae of the northern species of *Entoprocta* (cf. also the figures in Marcus l. c., pp. 8–9). Their size, viz. up to 400 μ as the largest diameter in *Pedicellina*-larvae and up to 300 μ in *Loxosoma*-larvae, shows that they may be easily caught by our nets generally used for collecting the main series, and that if they were fairly frequent they have hardly been overlooked in our samples. In spite of this, larvae of *Pedicellina* have not been observed at all in our samples, but they may have been overlooked in a few specimens, while some few larvae of *Loxosoma* were observed in a few samples of the main series taken off Ven. Unfortunately, the dates of occurrence have not been noted and it is unknown to which species the larvae should be referred. However, a main series taken off Helsingør on $^{17}/_{8}$-42 contained a single larva, which was carefully sketched (fig. 86). It agreed closely with Barrois' figure (1877 a, pl. 1 fig. 14) of the larva of *Loxosoma singulare*. As this larva is rather different from that of *Loxosoma phascolosomatum* (cf. Marcus 1940, p. 9, fig. 6 B), it can be taken for granted that our larva belongs to the former species. As the pelagic life of these larvae is very short, it seems natural to suppose that also the adults of *Loxosoma singulare* occur in the Sound or its nearest vicinity.

Ectoprocta.

The paper of Marcus (1940) in connection with those of Lönnberg (1898, 1899) mention 37 species of *Ectoprocta* from the Sound, viz. *Crisiella producta*, *Crisia eburnea*, *Tubulipora flabellaris*, *T. liliacea*, *Lichenopora hispida*, *L. verrucaria*, *Membranipora membranacea*, *M. pilosa*, *M. crustulenta*, *M. tenuis*, *M. unicornis*, *M. lineata*, *M. craticula*, *M. dumerilii*, *M. aurita*, *M. flemingii*, *Flustra foliacea*, *Scrupocellaria scabra*, *Cribrillina annulata*, *C. punctata*, *Hippothoa hyalina*, *Escharella immersa*, *E. ventricosa*, *Schizomavella linearis*, *Escharina spinifera*, *Microporella ciliata*. *Stomachetosella sinuosa*, *Porella concinna*, *Smittina trispinosa*, *Alcyonidium gelatinosum*, *A. polyoum*, *A. hirsutum*, *A. albidum*, *Flustrella hispida*, *Bowerbankia caudata*, *Valkeria uva*, and *Triticella pedicellata*. Four more species are known from the Kattegat as well as from the Baltic, five from the Kattegat as well as the Belts, and nine from S.E. Kattegat. It seems likely that several of these species have hitherto been overlooked in the Sound.

Excellent papers on the larvae of *Ectoprocta* have been published by Barrois (1877 a), Lohmann (1904, 1911), Prouho (1890, 1892) and several other authors. Most of the northern larvae figured in these papers were reproduced by Marcus (1940). — Ecologically the larvae of *Ectoprocta* belong to two distinct groups, viz.

1. Larvae originating from egg-laying parents, characteristic by bearing calcareous plates on the sides of their compressed bodies, by having a well developed intestine by means of which they feed from the plankton, and by having a long pelagic life (according to Marcus l. c. p. 334, nearly two months). This larval type — the *Cyphonautes*-type — is known from the genus *Membranipora*, and from the species *Alcyonidium albidum* and *Flustrella hispida*.

2. Larvae mainly originating from viviparous parents, characteristic by containing a certain amount of yolk and by having a partially developed intestine or no intestine at all; thus they are independent of the plankton as a source of food. Their pelagic life is very short — up to 24 hours at the most (Marcus l. c., p. 334). Larvae of this type occur in most marine Bryozoans which have not larvae of type 1, that is to say in by far the majority of Danish species.

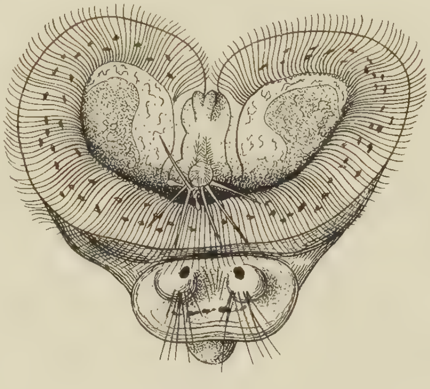


Fig. 86. Larva of *Loxosoma singulare* Kef. Seen from the ventral side. From plankton between Hellebæk and Kulla Gunnarstorp, depth 30—0 m, caught and drawn from life on $^{17}/_{8}$-1942. Drawn from a sketch by stud. mag. Erik Rasmussen.

The two types seem accordingly to correspond closely to the main types known from all other groups of marine invertebrates with a pelagic stage, viz. the planktotrophic type with a long pelagic life, and the lecithotrophic type with a short pelagic life. — As might be expected, the latter group is of no importance in the plankton, while the first-mentioned group — the *Cyphonautes* larvae — constitutes a large part of the whole larval stock in the Sound.

Lecithotrophic larvae with a short pelagic stage (cf. pp. 436—438) were taken in our main series off Ven on: $^{26-27}/_{9}$-36 (one larva), and off Helsingør on: $^{7}/_{10}$-41 (4 larvae of one species, and 2 larvae of another species), both having thus been taken in the autumn. Unfortunately the larvae have not been sketched, but they agreed with the larval types known in *Alcyonidium polyoum* and the genera *Escharina*, *Schizoporella*, and *Membraniporella* (cf. Marcus 1940, p. 341, fig. 186). As larvae of this type were directly sought for, they have hardly been overlooked in our plankton samples except for a few sporadic specimens.

Planktotrophic larvae with a long pelagic life, i. e. the *Cyphonautes* type, are, however, very common in the plankton, constituting off Ven 3.5 per cent of all the larvae of bottom invertebrates (45 main series) and off Helsingør 24.1 per cent (20 main series), i. e. 12.9 per cent in all the main series investigated from the Sound. The table on p. 372, and the graphs in fig. 193 (Ven) and fig. 194 (Helsingør) show their occurrence throughout the year. Off Ven the *Cyphonautes* larvae showed a distinct minimum in February-March, increasing slightly but varying in numbers in April to August-September, and reaching a large and spontaneous maximum in October to early January, with a summit in November-December (cf. the graph p. 375, other inv.). During January a sudden decrease set in, until the minimum was reached about the middle of February. Off Helsingør, where *Cyphonautes* larvae play a much greater part in the plankton, the minimum seems to occur in February to April, the number increasing, though with great variations, in May to September. Then, about the middle of October, the maximum sets in, to reach its summit in November to January with up to 6000 to 18000 larvae per main series. The number of larvae decreases rapidly during February, to reach a distinct minimum in March. As a characteristic feature of the conditions in the Sound it can thus be stated that larvae of *Cyphonautes* occur in all months of the year, with a minimum occurrence in late winter and early spring and a maximum occurrence in late autumn and early winter.

Ten species of *Membranipora* are known from the Sound in the adult stage, and since also other species known from the Sound, e. g. *Alcyonidium albidum* and *Flustrella hispida*, reproduce by larvae of the *Cyphonautes* type, a large number of different *Cyphonautes* larvae may be expected to occur in the plankton. — In our samples, however, we have only been able to distinguish four different species of *Cyphonautes*, two of which are extremely common, while the other two are rather rare. One of the common species could be readily identified without any difficulty as the

Larva of *Membranipora pilosa* (= *Cyphonautes compressus*), cf. fig. 87 A: The latest pelagic stage is of a dark yellowish-brown colour, very opaque, and rather thick. The posterior edge of the smooth shells is much shorter than the anterior, the shape of the shells being that of an oblique triangle, somewhat higher than broad, with rounded oral corners. The oral edge of the shell has a length of about 480 to 490 μ. The stomach and hindmost part of the intestine are of a greyish-brown colour. Our larva (fig. 87 A) agrees closely with the old larva of *Membranipora pilosa* figured by Barrois (1877 a, pl. 15, fig. 3), which is in good agreement with its frequency in the Sound plankton. The figures of Barrois (l. c., pl. 15, figs. 1—2) show that the shells of younger larvae are less oblique, and this feature was also observed in larvae in the Sound. — Larvae of *M. pilosa* constitute nearly half of the stock of *Cyphonautes* larvae in the Sound. They occur throughout the year with a pronounced maximum in (November) December-January. Thus, in a main series taken off Helsingor on $^{19}/_{12}$-41 the larva constituted 95 per cent of the 6100 *Cyphonautes* larvae. Larvae from the same localities taken on $^{11}/_{11}$-41 and $^{3}/_{1}$-42, adhering to the bottom of the Petri dishes, were observed to spread their shells and form the first two polypides. A bottle-collector exposed off Ven, depth 16 m, from $^{5}/_{7}$—$^{27}/_{8}$-39, i. e. for seven weeks, contained a young colony of 40 polypids of *Membranipora pilosa*.

Cyphonautes balticus Lohm., cf. fig. 87 B: The oldest pelagic stage is yellowish or colourless, quite transparent, and very thin. The smooth shells are triangular in shape with a rounded, protruding posterior corner of the oral edge. The anterior edge is somewhat longer than the posterior, and is faintly convexly curved, the shells being less oblique than those of *M. pilosa*. Apart from two groups of reddish-brown cells, one of which lies near the stomach the other just above the pear-shaped organ, the animal is quite colourless and transparent. The oral edge of the oldest larvae has a length of 600 to 680 μ, thus being much larger than those of *Membranipora pilosa*. The larva in question seems to agree on all points with Lohmann's description and figure of *Cyphonautes balticus* (here taken from Marcus 1940, p. 336, fig. 177). The truncated "apex", the protruding rounded corner at the transition from the oral edge to the posterior edge, and the transparent appearence seem to be common features of our larva from the Sound and of *Cyphonautes balticus* as recorded in the literature. Marcus (l. c., p. 336), however, describes the larva of *Cyphonautes balticus* as smaller (oral edge 210—390 μ long) than that of *Membranipora pilosa* (oral edge 430 -485 μ), while our larva from the Sound is much larger (oral edge 600—680 μ) than that of *M. pilosa*. Fig. 177 in Marcus

(l. c.), which represents *Cyphonautes balticus,* is, however, 405 μ along the oral edge, i. e. 15 μ longer than the maximum length given for the species by the same author in the same paper — a fact which supports the conjecture that Marcus's measurements do not refer to fully developed larvae. — *Cyphonautes balticus* is extremely common in the Sound plankton, constituting more than 50 per cent of all the *Cyphonautes* larvae found there, i. e. still commoner than the larva of *M. pilosa.* Hence it seems very likely that the larvae in question belong to *Membranipora membranacea,* the commonest species of *Membranipora* in the Sound. — *Cyphonautes balticus* occurs in the Sound throughout the year, it is the dominant *Cyphonautes* during the summer months, and shows a pronounced maximum in October-November, i. e. about one month earlier than the maximum of the larvae of *Membranipora pilosa.* A main series taken off Helsingør on $^{11}/_{11}$-41 contained 18400 *Cyphonautes,* 90 per cent of which belonged to *C. balticus,* while a similar main series taken one month later ($^{19}/_{12}$-41) contained 6100 *Cyphonautes,* 95 per cent of which belonged to *Membranipora pilosa.* — Several larvae of *C. balticus* taken on $^{11}/_{11}$-41 metamorphosed in our Petri-dishes during examination.

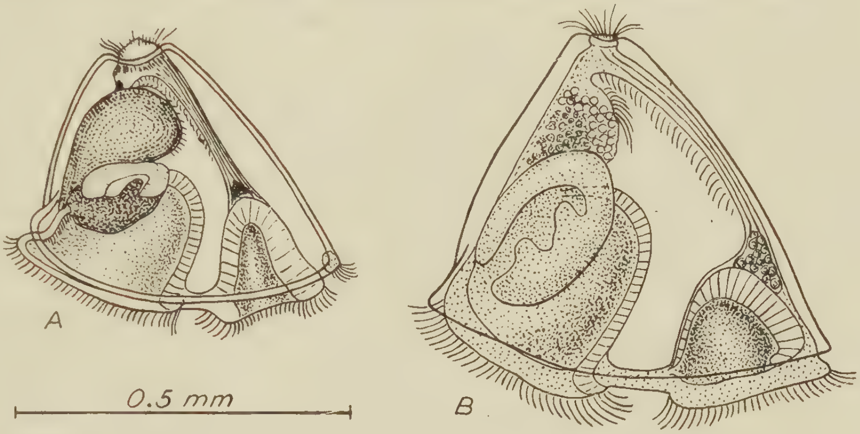


Fig. 87 A-B. *Cyphonautes* larvae from plankton off Ven, depth 18—0 m, caught and drawn from life on $^{4}/_{8}$-1938. Seen from the right side. — *A.* Old larva of *Cyphonautes compressus* Ehrbg. (= the larva of *Membranipora pilosa* (L.)). — *B.* Old larva of *Cyphonautes balticus* Lohm. (presumably the larva of *Membranipora membranacea* (L.)).

Cyphonautes barroisi Lohm. Good figures are given by Lohmann (cf. Marcus 1940, p. 336, fig. 178). Unfortunately this larva has not been sketched from the Sound. Shells triangular to rounded-oval, granulated over the whole surface, opaque and dark-brown in transmitted light. The larva is small, oral edge 160—200 μ long, easily recognisable and very characteristic. — *C. barroisi* is rather rare in the plankton. Off Ven it was found on $^{28}/_{1}$-39, and off Helsingør on: $^{11}/_{11}$-41; $^{2}/_{12}$-41; $^{31}/_{1}$-42; $^{20}/_{6}$-42; $^{17}/_{8}$-42, and $^{5}/_{9}$-42, thus occurring throughout the year with a maximum in winter. Only a few specimens per main series were found. The larva in question should most probably be referred to *M. crustulenta* (cf. Marcus l. c., p. 336), but no direct proof can be given.

Cyphonautes larva with a concavely curved posterior edge. Only observed on one occassion, viz. off Helsingør on $^{19}/_{12}$-41. No figures are available. Much smaller than the *Cyphonautes balticus,* but like this compressed, thin, transparent and yellowish or colourless, with smooth shells. The posterior and anterior edges of the triangular shells are longer than the oral edge, and the concavity formed by a pronounced curve of the posterior edge gives the triangular shells a rather high appearance and an acute "apex". — This larva is described here for the first time. Its identity is unknown. It seems to be rather rare in our plankton, but a few specimens may now and then have been confused with young *Cyphonautes balticus.*

Cyphonautes larvae seem to be rather resistant to changes in the temperature and salinity. They present a good and interesting subject for future investigations in the laboratory as well as in nature.

6. Placophora.

Five species of Chitonids are known from the Sound, viz. *Chiton* (*Tonicella*) *marmoreus* Fabr., C. (*Trachydermon*) *cinereus* L., *C.* (*Trachydermon*) *ruber* L., *C.* (*Trachydermon*) *albus* L., and *C.* (*Craspedochilus*) *marginatus* Penn, (Collin 1880, Lönnberg 1898, Petersen 1888, and Nierstrasz and Hoffmann 1924).

As regards Chitonids no observations on the reproduction are available from the Sound, and no larvae have been found in our four-year main series from Ven and Helsingør.—As this paper has to serve as a provisional handbook on larvae of bottom invertebrates from Danish waters, it seems reasonable, however, to briefly summarise what is known at present about the reproduction of each single species living in the Sound.

Chiton (Tonicella) marmoreus Fabr. Northern and middle parts of the Sound, not very common. — Lyngnes (1924) has described and figured a newly spawned egg from Norway (breeding in summer). The egg measures 210 μ in diameter excl. of the curious egg membrane, which bears densely crowded, cup-formed appendices over its whole surface. The spawning habits and the larvae seem to be unknown.

Chiton (Trachydermon) cinereus L. Common throughout the Sound at fairly great depths — Studied by Clark (1855), Lyngnes (1924), v. Knorre (1925), and Hoffmann (1931). (The studies of Lovén (1856), Garnault (1888), and Schweikart (1905) on "*Chiton cinereus*" refer to *Chiton* (*Craspedochilus*) *marginatus*). — Breeding in Oslofjord in summer, at Heligoland in August-November. The males are the first to spawn and the females will follow immediately afterwards. When spawning, the animals elevate the posterior end of their margin, and sperm and eggs respectively are carried out with the water stream from the gills. The eggs are shed singly, one egg from the right and one from the left oviduct, and so on. At Heligoland the eggs are shed freely in the water (Hoffmann l. c.) or they are retained between the margin and the gills of the mother animal, where they develop into embryos (v. Knorre l. c.). At the Norfolk coast 1300 to 1500 eggs spawned within 15 minutes or more by a single female will adhere to each other and to a substratum by their somewhat sticky, gelatinous egg membranes, thus forming a common batch. The individual egg is spherical, 200—210 μ in diam. excl. of the egg membrane, and 255—300 μ when this membrane is included. The spherical to egg-shaped larvae with a thin tuft of cilia in front, a ciliary ring round the middle of the body, and two small eyes hatch two to three days after having been spawned. They swim with great vivacity, and a few hours later they attain the shape of a *Chiton*, and the four to seven anterior valves can be distinguished on the dorsal side. The swimming larva takes no food from the plankton, i. e. it is lecithotrophic, and the whole pelagic life lasts from six hours to four days. — The varying mode of depositing the ova, viz. freely in the water, in batches adhering to a substratum, and by brood-protection, seems of slight significance only, as the embryos always hatch in the same stage of development. The retaining of some eggs between the margin and the gills of the mother animal may hardly be regarded as a true brood-protection, but seems to be related to the phenomena known for the Lamellibranchs *Mya arenaria*, *Mya truncata*, *Zirphaea crispata*, and *Cuspidaria cuspidata* (cf. pp. 419—420), which accidentally are known to retain fertilised eggs in their mantle cavity, where they will cleave and develop.

Chiton (Trachydermon) ruber L. Northern part of the Sound, rare. — Reproduction unknown.

Chiton (Trachydermon) albus L. Northern and middle parts of the Sound. Not common. — LYNGNES (1924) describes and figures a ripe egg, which, however, was still not spawned but was dissected out of the ovary. It measured 295 μ in diameter excl. of the egg membrane, thus being much larger than the eggs of *C. marmoreus*, *C. cinereus*, and *C. marginatus*. This seems to indicate a still shorter pelagic life than is known for the other Danish species, but the spawning and the larvae have not been studied.

Chiton (Craspedochilus) marginatus PENN. Northern and middle parts of the Sound. Not common. — LYNGNES (1924) has described and figured the newly spawned egg, and his figures show clearly that the studies of LOVÉN (1856), GARNAULT (1888), and SCHWEIKART (1905) refer to *Chiton marginatus* (not to *C. cinereus*). Breeding in summer near Norway. The newly spawned egg is 175—210 μ in diameter excl. of the egg membrane, which (like the egg of *C. marmoreus*) bears densely crowded, cup-formed appendices over its whole surface. Along the Swedish W.coast specimens kept in aquaria deposited their ova on small stones (season unknown). Seven to sixteen eggs were united into a batch by a slight adhesion of their egg membranes. The hatching young, 180 μ long, are very similar to those of *C. cinereus* (which see). Soon afterwards the larvae are in the swimming-crawling stage, and the seven anterior valves can be distinguished on the dorsal side. The larva now adheres to a substratum and soon attains its adult shape. During the pelagic life the larva takes no food from the plankton, i. e. it is lecithotrophic.

The facts given above seem to show that Danish Chitonids have a pelagic larval life from six hours to a few days only. They take no food from the plankton and do not metamorphose, the larva gradually attaining its adult shape. The paucity of adults of this group living in the Sound, the rather small number of eggs per spawning, and the very short pelagic life explain why the larvae have not been observed in our main-series from the Sound.

7. Prosobranchia.

The following authors have contributed to our knowledge of the distribution of the Prosobranch fauna in the Sound: ØRSTED (1844), MØRCH (1871, all earlier literature discussed here), COLLIN (1880), PETERSEN (1888, 1911, 1913, 1914, 1915, 1918), LÖNNBERG (1898, 1899), and MUCHARDT (1917). The papers of COLLIN (1880), PETERSEN (1888), and LÖNNBERG (1898, 1899) should be regarded as the main works dealing with the Sound. — During the last few years our investigations have added nine new species to the fauna of this area, viz. *Alvania punctura* (old larvae), *Coecum glabrum* (larvae which had commenced to metamorphose and crawl), *Triphora perversa* (one adult spm. and larvae), *Odostomia conoidea* (old larvae only), *Amauropsis islandica* (half-grown bottom stage), *Nucella lapillus* (adult animal), *Nassa incrassata* (several adult animals), *Philbertia linearis* (old larva only), and *Mangelia attenuata* (old larva). Thus, at present, 69 species of *Prosobranchiata* are known in living specimens from the Sound.

Our knowledge of the eggs and larvae of the Prosobranchs has been considerably increased through the literature of the last decade. Especially the papers of MARIE LEBOUR (1931c, 1932, 1933a-d, 1934a-b, 1935a-c, 1936 and 1937a), in which the majority of the Prosobranch larvae found off Plymouth are described and figured, are of the greatest value for our investigations in the Sound, having directly helped us to identify or to "trace" the identity of several larval forms. As to other larvae, however, LEBOUR's figures and descriptions are not sufficiently detailed to allow of a direct identification, and in several such cases we have had to clear up the identity of our larvae exclusively, or nearly exclusively, on the basis of our own observations, in spite of the available literature. — Several other authors have also contributed to our knowledge of the reproduction of the northern Prosobranchs. As the main papers I regard those of ANKEL (1926 to 1938), HERTLING (1928 to 1932b), GERSCH (1936), LINKE (1933a-b, 1934), ODHNER (1914a), PELSENEER (1906a, 1911 to 1926a), and THORSON (1935, 1940a, b). Valuable investigations have further been published by BONDESEN (1940), BOUTAN (1898, 1899), DELSMAN (1912, 1913, 1914), FISCHER (1892), GALLIEN & LARAMBERGUE (1936, 1938), HENKING (1894), MEYER & MÖBIUS (1872), PORTMANN (1925, 1926, 1927, 1930a, b), RASMUSSEN (1944), ROBERT (1902), SMIDT (1938, 1944), TATTERSALL (1908, 1920), KAREN VESTERGAARD (1935), and several other authors. LEBOUR (l. c.), however, is the only author who has hitherto tried to clear up the conditions of reproduction and development for a whole Prosobranch fauna within a limited area.

The figures have been drawn by the author. It was my intention to sketch the larvae in swimming stages as well as withdrawn in their shells, and as many characteristic details as possible are given. Larvae from fresh plankton, when irritated by the unnatural conditions, will often rest on the bottom of the Petri dish with the velum and the whole animal withdrawn in their shells; detailed sketches of larvae in these stages may often also contribute to the identification of larvae fixed in alcohol or formalin.

Furthermore, for some genera, e. g. within the *Pyramidellidae*, the larvae of which are still unknown and undescribed, the type of the apex (cf. pp. 199—207) has shown whether the larval development is non-pelagic or the larva has a short pelagic or a long pelagic stage.

Emarginula fissura (Linné). One living specimen found off Ellekilde (Collin 1880), several empty shells.

Reproduction: Unknown in the literature. No observations from the Sound.

Acmaea testudinalis (O. F. Müller). Middle and northern parts of the Sound, rather common.

Reproduction: A. Literature. Aurivillius (1898b) has observed ripe eggs and ripe sperms in this species in the spring at Kristineberg. Mary Willcox (1905) gives the following data on the reproduction near New England: Spawning from April to July (September). The eggs are not dropped separately, but are "imbedded in a layer of very thin mucus, in which they lie one layer deep and at regular distances apart". Egg diameter $^1/_5$ mm. A Trochosphere is developed the day after the eggs have been spawned. No figures are given, and the development has not been watched. Young bottom stages originating from larvae of the same season reached a length of four to five mm already in September-October. The older larval stages are still unknown.

B. Own remarks. Plankton samples from 30—0 m taken between Hellebæk and Kulla Gunnarstorp, on $^{20}/_6$-42, contained a single larva (fig. 88) already able to crawl. Larvae of this type have never been observed in our earlier samples, where they have probably been confused with Nudibranch larvae. The shell was also very similar to those of various Nudibranchs, but the shell as well as the animal inside it were quite symmetrical, the latter moreover with a distinct mantle and a large cephalic lobe — all characters which point to the *Patellidae*. The coecal-like — not coiled nautiloid — shell with its minutely granulated surface, its slight dorsal flexure and a groove on each side agrees in all details with the embryonic shell found on the top of a young *Acmaea testudinalis* in the crawling stage less than half a millimeter in length, described and figured by Morse (1910, pp. 314—15, figs. 2, 3 and 4). The animal in Morse's specimen (l. c. fig. 2) is also in close agreement with the larval animal from the Sound. The shell seen on the top of the just metamorphosed *Patella vulgata* (Lebour 1937a, fig. 1 f) also shows the closest similarity in shape (bilateral symmetry) as well as structure (minute granulations) to that figured here. The figure of Pelseneer (1906b) showing a pronounced coiled nucleus in *Patella vulgata*, and the statement of Fisher (1904), that "The *Acmaeidae* possess a larval nautiloid shell", have, accordingly, proved to be erroneous. The embryonic shell in both genera has the shape of a blunt coecal-like cap without any suggestion of a coil.— As *Patella* is absent from the Sound it seems reasonable to refer the larva in question to *Acmaea testudinalis*, especially since the larva of *Helcion pellucidum* is well known, and *Lepeta coeca*, as far as can be judged, has a non-pelagic development.

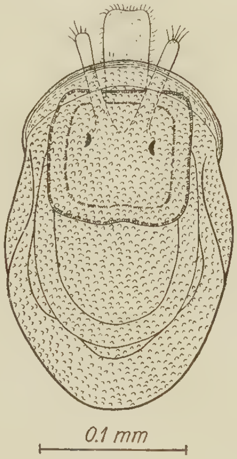


Fig. 88. Larva belonging to *Acmaea testudinalis* (O. F. Müller) (see the text p. 163). From plankton between Hellebæk and Kulla Gunnarstorp, depth 30—0 m, caught and drawn from life on $^{20}/_6$-1942.

The larva in question (fig. 88) has two large tentacles, a much prolonged forepart of the foot, two black eyes, two reddish-brown borders of pigment along the cephalic lobe, but otherwise it is quite colourless. In spite of its tiny size it was already able to crawl, its pelagic life may be supposed to be rather short, and probably it takes no nourishment from the plankton. On $^{5}/_{9}$-42 the plankton in the same locality contained one more larva which in shape as well as in size bore a close resemblance to that figured here.

Acmaea virginea (O. F. Müller). Middle and northern parts of the Sound, not common.

Reproduction: A. Literature. Boutan (1898, 1899) gives the following data from Roscoff: Spawning in April-May. The sexual products are shed freely in the water, where the eggs will spread immediately. The shell is formed two days after fertilisation. The development was followed until metamorphosis, but neither a description nor figures are given. Nothing is mentioned concerning the length of the pelagic life. — Ankel (1938a, p. 5) mentions that the absolute size of the embryonic shells varies considerably from specimen to specimen in this species.

B. Own remarks. Nothing is known about the reproduction in the Sound.

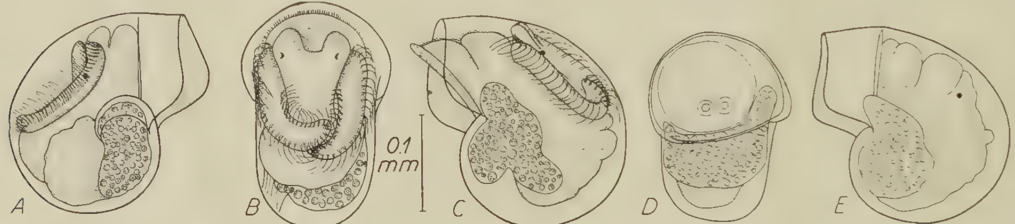


Fig. 89 A-E. *Helcion pellucidum* (Linné). Larvae from plankton off Frederikshavn (NW. Kattegat), depth 10—0 m, caught and drawn from life on $^{8}/_{8}$-1939, Seen from the right side (A), the dorsal side (B), the left side (C), and the ventral side (D).—*E*. Larva with reduced velum. Accordingly slight growth only seems to take place in the planktonic stage.

Helcion pellucidum (Linné). Rather common in the northern part of the Sound, found especially on *Laminaria* at fairly great depths along the Swedish coast.

Reproduction: A. Literature. Ankel (1936a) reports from Heligoland that ripe specimens sitting near each other spawn sperms and eggs freely in the water, where they will sink to the bottom of an aquarium, but under natural conditions will probably be kept floating in the water masses by the movement of the water. Lebour (1937a) describes and figures the egg, which is 320 μ across, and the pelagic larval stage. First a *Trochophora* is formed, then a shelled *Veliger*, 160—180 μ across the larval shell. This shell has a large outer lip, the margin of which is overlapping on both sides, so that the mouth of the shell looks like the hood of a perambulator. Larvae of this type have been found in the plankton near Plymouth in almost all months of the year.

B. Own remarks. Larvae of this species are very common in August plankton from N.W. Kattegat (Frederikshavn), where the sketches in fig. 89A—E were drawn. From the Sound only a single larva is present, taken off Ven, 18—0 m, on $^{23}/_{8}$-38, but the species has probably been overlooked several times prior to that date, whereas careful search after this first finding gave a negative result. The larval shell is glassy, the animal itself is yellowish to olive-green, and the liver is greyish. The larvae figured here are among the largest known from the Danish plankton; they had already large tentacles, and the velum was rather small; they were probably very near the stage of metamorphosis. The pelagic life seems thus to be very short.

Lepeta coeca (O. F. Müller). Middle and northern parts of the Sound, not uncommon locally on stones at fairly great depths.

Reproduction: Unknown in the literature. The very frequent, nearly dominating occurrence of this species in the large East Greenlandic fjords, where not a single larval Prosobranch was present in our large series of regular plankton hauls taken during a whole year, seems to support the conjecture of a non-pelagic development of this species.

Pilidium fulvum (O. F. Müller). Northern part of the Sound, very rare.

Reproduction: Unknown in the literature. No observations from the Sound.

Calliostoma miliare (Brocchi) (= **Trochus millegranus** Phil.). Not rare off Knähaken in the northern part of the Sound.

Reproduction: A. Literature. Jeffreys (1865, p. 326) states that the "fry" has an umbilical perforation. Nothing is known about the spawning and the larval development, but the two species of *Calliostoma* hitherto examined, viz. *C. zizyphinum* and *C. papillosum,* like those of the closely related genus *Cantharidus*, viz. *C. striata* and *C. exasperatus,* to which genus the species in question is referred by some authors, are known to spawn their eggs in gelatinous masses, from which the young hatch in the crawling stage (cf. Lebour 1937 a). It seems most likely, therefore, that *Calliostoma miliare* develops in the same way, without any planktonic larval life.

B. Own remarks. Nothing is known about the reproduction from the Sound.

Gibbula tumida (Montagu). Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. Gersch (1936) describes the spawn from Heligoland (where the breeding season, according to Ankel (1936 a), is March to April): The eggs are yolky, greenish, 182 μ across, 140 μ across the egg-cell, and are deposited in irregular, transparent, gelatinous masses. Fertilisation takes place in the water. The individual egg mass contains from 142 to 160 eggs. Often "faecal pellets" of the mother animal are included in the slime. The young hatch in the crawling stage, and the "fry" (according to Jeffreys 1865, p. 309) has often pink spiral lines on the shell.

B. Own remarks. Nothing is known about the reproduction from the Sound.

Gibbula cineraria (Linné). Throughout the Sound, not very common.

Reproduction: A. Literature. Robert (1902, p. 288) describes the spawning at Roscoff in June and mentions the development; however, no figures of the larva are given. Gersch (1936) gives the following data from Heligoland in March-April: The yolky, greenish eggs, 178 μ across, the egg-cell proper 144 μ across, are shed singly in the water, where fertilisation takes place. The larval stage is pelagic, but still undescribed and unfigured. Lebour (1937) states that ripe eggs may be found in the females in almost any month of the year.

B. Own remarks. Nothing is known about the reproduction in the Sound.

Neritina fluviatilis Linné. Southernmost part of the Sound (Saltholm, the South harbour of Copenhagen, Køge Bugt, Kokkedal near Nivaa), common. Isolated specimens in the tidal zone off Ven.

Reproduction: A. Literature. Claparède (1857) and Blochmann (1882) describe the egg capsules and development of the fresh-water form. Lindström (1855) describes the development of the Baltic form, and Bondesen (1940) describes the egg capsules and embryos of this species from the Sound. The egg capsules, 700—900 μ across, are laid on stones or *Fucus vesiculosus*. Each capsule consists of two parts, viz. a lower part shaped like a saucer and an upper part forming a dome-shaped cover over the lower part and united with this along a thickened margin. The capsules are at first yellowish-white, rather soft, later on they grow yellowish-brown and rather hard. In the Sound each capsule contained 40—66 eggs (capsules from fresh-water lakes may be much larger, viz. 900—1200 μ across, and contain 70—160 eggs per capsule). The uncleaved eggs of the Saltholm population measure 110 to 125 μ in diameter. Only one of the eggs develops into an embryo, all the other eggs serving as food for that embryo. The young hatch in the crawling stage without any pelagic life.

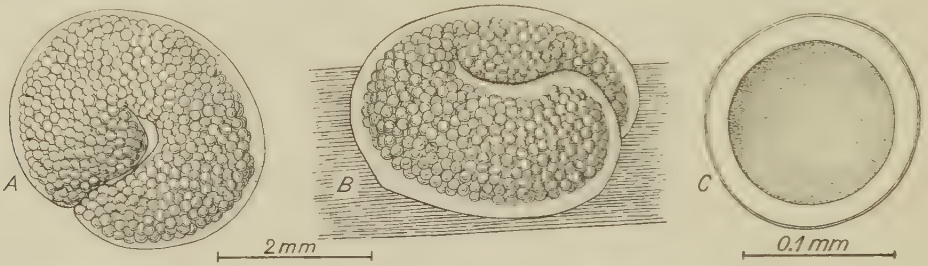


Fig. 90 A-C. *Lacuna divaricata* (O. Fabricius). Egg-masses taken on *Fucus serratus* off Aalsgaarde, depth 2—3 m, on $^{4}/_{4}$-1945. Drawn from life on the same day. — *A*. Egg mass of medium size with uncleaved eggs; seen from above. — *B*. Somewhat larger egg-mass with uncleaved eggs in lateral view. — *C*. A single uncleaved egg.

B. Own remarks. On March 26th, 1939, several egg masses with large living embryos inside were taken on *Fucus vesiculosus* which drifted up through the Sound off Ven. They had undoubtedly come from the southern part of the Sound, as there was a north-going current. On October 7th, 1941, egg capsules, likewise with large embryos, were taken under quite similar conditions off Hellebæk in the northernmost part of the Sound. The egg capsule of this species, which is associated with fresh or brackish water, seems thus to be fairly resistant to sea water of a higher salinity, and when during their drift through the Sound and southern Kattegat such fragments of *Fucus* are washed ashore in a bay with brackish water or a similar locality, the species will have a good possibility of settling there.

Lacuna divaricata (O. Fabricius). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. The egg masses and larvae are described and figured by Meyer & Möbius (1872), Delsman (1913), Hertling & Ankel (1927), Hertling (1928, 1931), and Lebour (1937a). The results of all these investigations are briefly as follows: Breeding season near Heligoland in January to June, at Plymouth in January to May, and in the Zuidersee in spring (Havinga 1922, p. 388). The spawn, which is laid on *Zostera*, *Laminaria*, and *Fucus*, is of a creamy colour and is formed as a very slightly spiral, gelatinous ring. Newly laid egg masses measure 2 to 3 mm in diameter, but as the larvae develop, the volume of the egg mass increases considerably, the largest diameter reaching a length of 4 to 6 mm (exceptionally 9 mm). Each spawn contains 1000—1200 eggs. The individual egg, 103 to 128 μ across, is included in an egg cocoon, 125 to 147 μ across. As the larvae develop, the spawn will become more transparent and softer. The young hatch as Veligers after having spent 15 to 26 days in the egg mass (according to the prevailing temperature). When hatching, the Veligers figured by HERTLING (1931) have a transparent shell with one and a half whorls, a bilobed velum with brownish-red marginal pigment, two black eyes, otocysts, foot and operculum, and are able to feed on the plankton. They stay for some time in the plankton, where they grow rather much and metamorphose when the shell has developed two and a half whorls.

B. **Own remarks.** Out of fifteen egg masses of this species taken on *Laminaria* off Helsingør at a depth of 20 m on $^{2}/_{4}$-42 after a heavy ice-winter, nine contained embryos not yet rotating, one had rotating embryos, and five contained shelled Veliger-larvae, which in two of them were just ready to emerge. The latter egg masses had thus been spawned at the beginning or the middle of March.

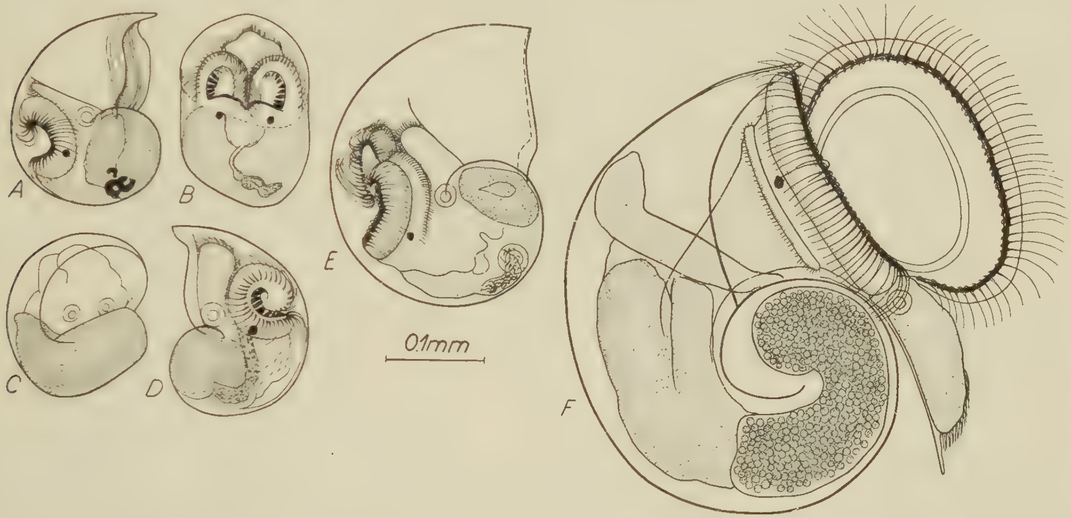


Fig. 91 A-F. *Lacuna divaricata* (O. FABRICIUS). Planktonic larvae. — *A* to *D*. Larvae from egg-mass taken off Snekkersten on *Laminaria*, depth 20 m, on $^{2}/_{4}$-1942. The larvae hatched from the egg-mass on $^{2}/_{4}$-1942 and were drawn from life on the same day. Seen from the right-side (A), the dorsal side (B), the ventro-lateral side (C), and the left side (D). — *E*. Medium-sized larva from plankton between Hellebæk and Kulla Gunnarstorp, depth 35—0 m, taken on $^{10}/_{4}$-1942 (drawn from life on $^{12}/_{4}$-1942); seen from the right side. — *F*. Old larva from plankton off Frederikshavn (NW. Kattegat), depth 4—5 m, caught and drawn from life on $^{1}/_{7}$-1937.

In 1943, when the winter was very mild, two egg masses were taken on *Laminaria* off Snekkersten on $^{1}/_{3}$. One of them contained rather young cleaving-stages, the other briskly rotating embryos. On $^{4}/_{4}$-45 egg masses with undeveloped eggs (fig. 90 A-B) as well as with young Veligers were abundant on *Fucus serratus* at a depth of 2 m off Aalsgaarde. As late as $^{1}/_{7}$-41, $^{3}/_{7}$-42, and $^{7}/_{7}$-42 several egg masses, some of them with young eggs, were observed on *Fucus* and *Laminaria* off Helsingør. As late as $^{18}/_{7}$-42 and $^{18}/_{7}$-1945 a few egg masses, some of them with young eggs, others with older embryos, were found on the Hittarp-reef, at a depth of 15 to 20 m, but on $^{28}/_{7}$-41 a large number of *Laminarians* from a depth of 15 m on the Hittarp-reef (where adult specimens of *Lacuna* were common) were examined carefully, but not a single spawn was found, and the same was the case in other localities investigated later in the summer. — In the Isefjord egg masses were seen on *Fucus serratus* on $^{5}/_{6}$-43. Uncleaved eggs from Aalsgaarde taken on $^{4}/_{4}$-45 (fig. 90 C) measured about 110 μ across the egg cell proper and about 140 to 145 μ across the egg-cocoon. An egg mass of medium size contained about 1450 eggs.

The occurrence of the larvae in plankton agrees well with the data found for the eggs. Larvae were found in our samples taken off Ven on: $^{6}/_{6}$-37 (1 spm.); $^{23}/_{7}$-37 (3 spms.); $^{18}/_{4}$-38 (18 spms.); $^{10}/_{5}$-38 (70 spms.); $^{6}/_{6}$-38 (14 spms.); $^{18}/_{6}$-38 (4 large spms.); $^{1}/_{7}$-38 (6 spms.); $^{17}/_{5}$-39 (55 large spms.); $^{4}/_{6}$-39 (5 large spms.); $^{17}/_{6}$-39 (1 large spm.); $^{3}/_{7}$-39 (3 large spms.); $^{15}/_{7}$-39 (3 spms.), and $^{5}/_{8}$-39 (2 large spms.), and off Helsingør on: $^{10}/_{4}$-42 (107 spms.); $^{27}/_{4}$-42 (40 spms.); $^{15}/_{5}$-42 (33 old and young spms.); $^{4}/_{6}$-42 (1 large spm.); $^{20}/_{6}$-42 (1 large spm.); $^{6}/_{7}$-42 (2 large spms.); $^{18}/_{7}$-42 (5 large spms., some of them with carmine pigment along the margin of the velum as well as a spot of carmine pigment on each velar lobe); $^{25}/_{7}$-42 (1 large spm.), and $^{5}/_{9}$-42 (1 rather young spm.). Thus the larvae occur from early April to July (exceptionally to August, and very rarely to September). The older larval stages are only met with in May to July, and the pelagic life seems thus to be rather long. The larvae (fig. 91 A-F) are easy to recognise; they have a colourless, transparent shell twisted nearly in one plane, thus looking rather compressed in the older stages. The outer lip is protruded into a rather conspicuous process. The bilobed velum has claret-coloured marginal pigment, the eyes are black, the liver greyish-green, the intestine has a section with blackish pigment, and the stomach of the young specimens is reddish-brown. The largest diameter of the shell of the just hatched larva is 200 to 210 μ, while in larvae nearly ready to metamorphose the longest diameter of the shell is 470 μ. The larva of *Lacuna divaricata* is often the dominant Prosobranch larva in spring plankton in the Sound, until — in June, when the *Littorina littorea* maximum sets in — it is reduced to the commonest Prosobranch larva but one.

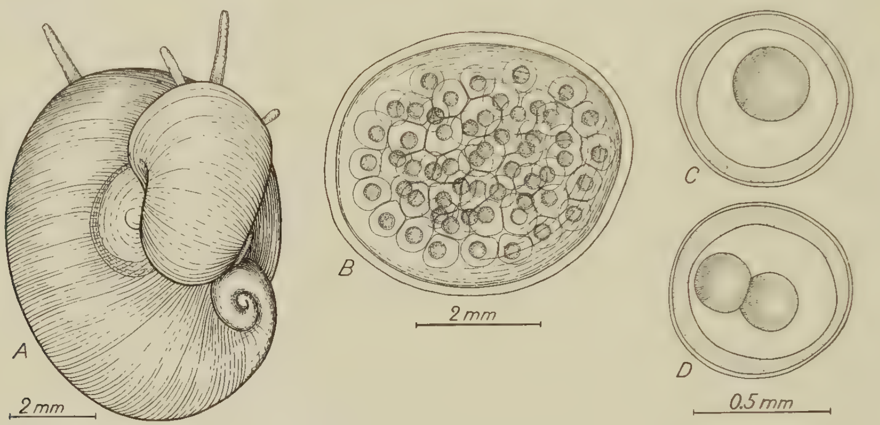


Fig. 92 A-D. *Lacuna pallidula* (DA COSTA). Animals and egg-mass taken on *Fucus serratus* off Aalsgaarde, depth 2—3 m, on $^{4}/_{4}$-1945 (drawn from life the same day). — *A*. Adult female with the dwarf-male attached to its shell near the genital opening. Operculum, foot and tentacles of the male are seen. — *B*. Egg-mass with uncleaved eggs, seen from above. — *C*. Single uncleaved egg. — *D*. Egg in the 2-cell-stage.

Lacuna pallidula (DA COSTA). Northern and middle parts of the Sound, not uncommon in the northern part on *Fucus*, *Laminaria*, and red algae.

Reproduction: A. Literature. The reproduction and egg masses figured and (or) described by PELSENEER (1911), HERTLING & ANKEL (1927), GALLIEN & LARAMBERGUE (1936 and 1938), and LEBOUR (1937 a) present the following main features: Breeding season at Wimereux and Heligoland (December) March-April (May-July). Pronounced sexual dimorphism in the adults. The weight of the female is ten times that of the male, which is often attached to the shell of the female near its mantle opening. The shells of the male specimens have a much broader columella than the female shells. The species is "annual"; ripe males originating from embryos in the spring are already present in November and will fertilise the females although the latter are not yet ripe. The males will then die the following spring somewhat earlier than the one year old females. The yellowish gelatinous spawn is laid on *Laminaria* and *Fucus.* It has an oval to circular shape, arching from the substratum like an inverted watch-glass, the largest diameter of the egg mass being 3900 to 5300 μ. It contains from 60 to 150 yellow eggs. The individual egg, 254—276 μ across, is included in an egg cocoon, largest diameter 529—571 μ, and all egg cocoons are imbedded in a slimy fluid, which is rather tough and coriaceous on the outer surface. The egg masses are rather similar to those of *Littorina obtusata*, which, however, are much larger, of a different shape, and have a much more hardened slime. The largest embryo figured (PELSENEER 1911, fig. 25) measures 515 μ (largest diameter of the shell) and is in the crawling stage, in which the young will normally hatch.

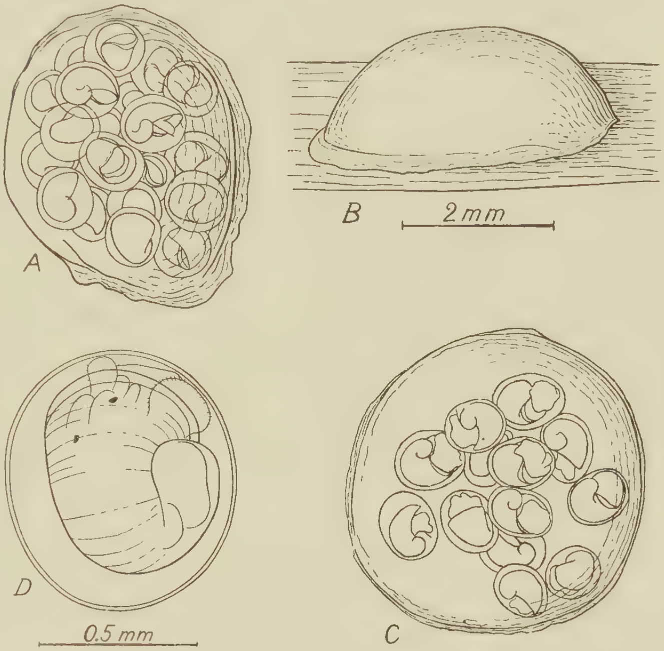


Fig. 93 A-D. *Lacuna pallidula* (DA COSTA). *A* and *B*. Egg-mass with 28 embryos taken off Helsingør, depth 25 m, on *Fucus serratus*, caught and drawn from life on $^{1}/_{7}$-1941. — *A*. Seen from above, the embryos showing through the egg-jelly. — *B*. The egg-mass in lateral view attached to the *Fucus*-leaf. — *C*. Egg-mass with 13 embryos nearly ready to hatch, taken on a leaf of *Delesseria* on Hittarps reef, depth ? m, on $^{7}/_{7}$-1941 (drawn from life the same day). — *D*. Single embryo in the egg-jelly; from the egg-mass fig. 93 A.

B. Own remarks. Off Aalsgaarde, at a depth of 2—3 m, five adult females were found on *Fucus serratus* on $^{4}/_{4}$-45. Two of them had dwarf-males attached to their shells (fig. 92 A). Nine egg masses were found on the same *Fucus*-plant, five of them with uncleaved eggs (fig. 92 B-C), two in the 2-cell stage (fig. 92 D), and two in the 16-cell stage. Thus the spawning seems to have just commenced. The nine capsules contained about 35—50—50—50—60—65—70—75 and 75 eggs and embryos respectively. The individual egg cell (270 to 300 μ across) was larger than those from France (254 to 276 μ). On $^{1}/_{7}$-41 two egg masses of this species were found off the point of Kronborg (Helsingør), 25 m depth, attached to *Fucus serratus*. One of them contained young eggs, and the other (fig. 93 A-B and D), the largest diameter of which was 4.1 mm, contained 28 embryos (largest diameter of the shell 700 μ), with a horn-coloured shell, a distinct foot, eyes and operculum, and a reduced velum. On $^{7}/_{7}$-41 two more egg masses were taken on *Fucus* and red algae near the Hittarp-reef, at depths of 16—20 m. One of them (fig. 93 C) was examined. The largest diameter of the egg mass was 4.25 mm, and it contained 13 embryos (largest diameter of the shell 700 to 750 μ), with black eyes, snowy-white liver (in direct light), and a nearly transparent shell with a very broad aperture. Finally, on $^{18}/_{7}$-42, two other egg masses were taken on *Fucus serratus* on the Hittarp-reef, depth 5–10 m. They were not closely examined. — Apart from the small number of eggs or embryos characteristic of all the egg masses examined, the features observed agreed entirely with those stated in the literature for *L. pallidula*, to which the embryos could be referred on the basis of a direct determination of their shells. These facts seem to show that in the Sound *L. pallidula* is represented by a small form which in the adult stage is somewhat smaller than specimens from shores near the ocean, and which spawns smaller egg masses with a much smaller content of embryos than those from more Atlantic localities. On the other hand, the hatching embryos in the Sound seem to be much larger (700 to 750 μ across the shell) than those observed near France (515 μ), which is in good agreement with the larger egg-size of the Danish specimens, but PELSENEER's measurements may refer to embryos which are not quite as old as those measured from the Sound.

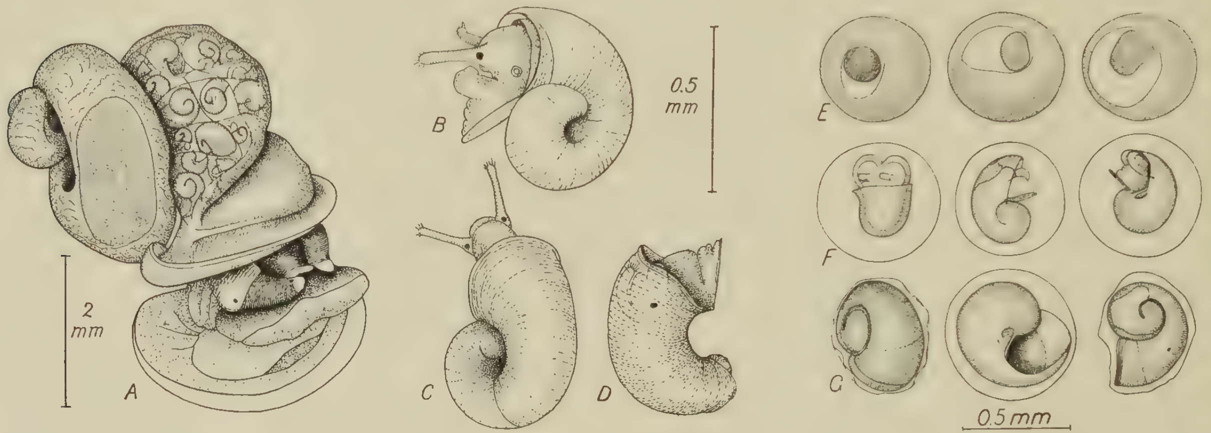


Fig. 94 A-G. *Littorina saxatilis* (OLIVI) var. *tenebrosa* MATON. — *A*. Adult female with the shell removed to show the embryos in the brood pouch. From the *Zostera*-vegetation off Ven, depth 1 m, caught and drawn on $^{11}/_{8}$-1942. — *B* to *D*. Sinistral and dentalioid embryos from the brood-pouch. Dissected out and drawn from life from a female taken off Ven on $^{1}/_{7}$-1943. — *E, F* and *G*. Embryos dissected out of the female fig. A to show the three different generations which are contained at the same time in a single brood-pouch, viz. rather undeveloped embryos, Veligers, and embryos nearly ready to hatch.

Littorina saxatilis (OLIVI). Throughout the Sound, common (main form and var. *tenebrosa* MTG.).

Reproduction: A. Literature. MIRIAM ROTHSCHILD (1940) states that the young are easily reared in captivity. PELSENEER (1911), DELSMAN (1914), LINKE (1933b, 1934), and ANKEL (1936a, p. 180) have described the reproduction and development, which can be summarised as follows: *Littorina saxatilis* is viviparous. The eggs, 200—205 μ across, each included in an egg cocoon 420 μ across, develop in a "breeding-room" in the oviduct, where they feed on the contents of white found in the egg cocoon. The breeding-room contains eggs and embryos the whole year round. Up to 900 eggs and embryos may be contained in a single breeding-room at the same time. Thus, a crowd of 28—37 eggs is transferred to the breeding-room 17 hours after copulation. A new copulation soon after is followed by a new crowd of eggs, and so on. Thus a single breeding-room may contain e.g. the following crowds at the same time:

uncleaved eggs, young Veligers, Veligers with shells, older Veligers with shells, eyes, statocysts, etc., and young hatched from the egg membrane and ready to leave the mother. Embryos in which the velum has already been reduced, will break the egg capsule with their radula and leave the mother animal as young crawling stages without any pelagic life. In the oldest embryo from a breeding-room figured in the literature (PELSENEER, fig. 23) the largest diameter of the shell was 354 μ. — AURIVILLIUS (1898 b) found young in the breeding-room at Kristineberg in August-September.

B. **Own remarks.** Females examined on Ven (fig. 94A) in the summers of 1936, 1937, 1938, 1939, 1942, and 1943, and at Helsingor in the summer of 1941 all contained eggs and embryos in their breeding-rooms. A stock of *Littorina saxatilis* var. *tenebrosa* taken off Ven on $^{2-4}/_{7}$-43, consisting of 22 males and 19 females, was carefully examined and showed the following conditions as to embryos in the breeding-room:

Groups of embryos contained in a single breeding-room.

Size of the female	Number of embryos in the breeding-room	Quite young embryos	Young veligers	Older veligers	Embryos in the crawling stage	Number of embryos with abnormal development
Large	108	..	×	×	×	0
—	83	×	×	×	×	0
—	57	×	×	..	×	0
—	135	×	×	×	×	4 shells
—	137	×	×	×	×	Several shells
—	44	×	×	×	×	0
—	57	..	×	×	×	0
Medium.............	95	×	×	×	×	0
—	4	..	..	..	×	0
—	55	×	×	×	×	4 shells
—	62	×	..	×	×	3 —
—	35	×	..	×	×	1 —
—	20	×	..	..	..	Twins
Small	24	..	×	×	×	0
—	19	..	×	×	×	1 shell
—	26	..	×	×	×	0
— 3 spms. without embryos.						

The females examined, which had reached the stage of reproduction, showed an average of 60 embryos per breeding-room. Often four "groups" of embryos were found in a single breeding-room, but in a single case only one "group" was present. Embryos of three different "groups" from the breednig-room of the female fig. 94 A are sketched in fig. 94 E-G. It is remarkable that 6 of the 16 females with embryos, i. e. 37.5 per cent, contained a certain number of embryos with abnormally developing shells (cf. fig. 94 B—D). Thus, planorbid, sinistral, or even "dentalioid" shells were found. Such conditions are not mentioned by LINKE (l. c.) from Heligoland, and the large percentage of abnormal embryos occurring in the Sound may probably be explained by the fact that the brackish-water form var. *tenebrosa* is a special ecological type which is capable of surviving under the poorest conditions, and lives at the surface of the Sound under conditions so near its extreme limit for life that it is approaching total degeneration. — The very small number of embryos contained in a single breeding-room as compared with the up to 900 embryos per breeding-room found near Heligoland (Linke l. c.) is also remarkable, and it seems surprising that in spite of its small production of young the stock found in the Sound is able to maintain its population. -The abnormal sinistral shells (fig. 94 B-C) are hardly of the "genetic type" known for other Gastropods, as all degrees of twisting from the normal dextral, through the planorbid, to the sinistral type may be found. Similar abnormal embryonic shells are known for instance in the North-American viviparous fresh-water prosobranch *Campeloma rufum,* which belongs to the *Viviparidae* (cf. Mattox 1935).

A stock of *Littorina saxatilis* var. *tenebrosa* taken at Lynæs harbour in the Isefjord on $^{15}/_{7}$-43, and consisting of 12 males and 16 females, showed the following conditions as to embryos in the breeding-room:

Groups of embryos contained in a single breeding-room.

Size of the female	Number of embryos in the breeding-room	Quite young embryos	Young veligers	Older veligers	Embryos in the crawling stage	Number of embryos with abnormal development
Large	505	..	×	×	×	0
—	164	×	×	..	×	Twins; 1 spm.
—	333	×	..	×	×	0
—	365	×	..	×	×	0
Medium.............	202	×	×	..	×	Twins; 1 spm.
—	135	×	..	×	×	1 shell
—	191	×	..	×	×	Twins; 1 spm.
—	98	×	..	×	×	0
—	63	×	..	×	×	0
—	214	×	×	..	×	3 shells
—	56	×	×	×	×	1 shell
—	42	×	..	×	×	0
—	0	..	..	..	..	..
—	0	..	..	..	..	..
Small	76	×	×	×	×	A few shells and twins
—	56	×	..	×	×	0

The salinity at the surface of the Isefjord is much higher and the conditions here as a whole much more marine than at the surface of the Sound. In accordance with this the Lynæs population is apparently much less degenerated than the population in the Sound. Thus at Lynæs the average number of embryos per breeding-room of females which have reached the age of reproduction is 156, i. e. $2^1/_2$ times as much as in the Sound. Four of the 12 females with embryos had a few specimens with an abnormal shell. Unfortunately, however, exact counts are not available either from the Sound or from the Isefjord, but it can be stated with certainty that the number of abnormally developing embryos in proportion to the number of normal embryos is much smaller in the Isefjord than in the Sound. — It was ascertained that the development as well as the size of the hatching young were just the same in the type-form as in var. *tenebrosa.* In the largest young found in the breeding-room (Ven, $^{20}/_{7}$-37, 4 m depth, *Zostera*) the largest diameter of the shell was 530—595 μ. The shell itself was horn-coloured with a reddish-brown columella and suture. The animals had black eyes and large tentacles and were very similar to the adults. — Twenty pairs of mating specimens of the type form of *Littorina saxatilis* examined at Frederikshavn, N.W. Kattegat, on $^{28}/_{7}$-36, proved to consist of 18 pairs ♂ × ♀ and 2 "pairs" ♂ × ♂. Thus here the normal mating of ♂ × ♀ seems to dominate totally over the abnormal type.

Littorina obtusata Linné. Throughout the Sound, common in the northern part.

Reproduction: A. Literature. The reproduction, egg masses, and development are described and partly figured by Baster (1762), Pelseneer (1911), Delsman (1912, 1914), Hertling & Ankel (1927), and Linke (1933 b). Their results are briefly as follows: Breeding-time near France: March to September; at Heligoland: main breeding in March to April, but egg masses are also found here in May to October. The gelatinous egg mass, attached to stones or *Fucus*, is flat, longish-oval, kidney-shaped, on an average 7 mm long and 3 mm broad, amber-coloured or quite colourless. The gelatinous slime is rather hard and fragile, and includes 90 to 150 egg capsules 550 μ across, each containing only one egg, 205 μ across, imbedded in a whitish fluid, which serves as nourishment for the embryo. The egg capsules are arranged in three planes one above the other, and are all in the same stage of development. Spawning takes place a few hours after copulation, normally in the night at flood-tide. At a temperature of 13°—14° C the embryos take three to four weeks to develop inside the egg capsules, and the young hatch in the crawling stage with a reduced velum and a shell quite similar to that of the adults. Aurivillius (1898 b) mentions gelatinous egg masses with eggs and embryos on *Fucus serratus* at Kristineberg in July to August and refers them correctly to this species.

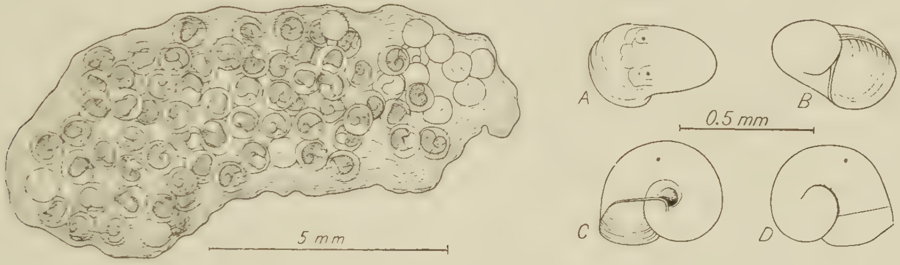


Fig. 95 A-D. *Littorina obtusata* Linné. Egg-mass with large embryos ready to hatch. The embryos had already hatched from the empty capsules. Taken on *Fucus serratus*, depth 10 m, on the Hittarp-reef, on $^{7}/_{7}$-1941 (drawn from life on the same day). — *A-D*. Embryos in the hatching stage. From an egg-mass taken on *Fucus vesiculosus* off Kristineberg (Bohuslän, Swedish W. coast) on $^{9}/_{9}$-1945 (drawn from life on $^{13}/_{9}$).

B. Own remarks. Off Aalsgaarde adults of this species were abundant on *Fucus serratus* at a depth of 2 to 3 m on $^{4}/_{4}$-45. In spite of a careful examination of several *Fucus* plants only a single egg mass was found, containing about 230 embryos in the 16-cell stage, i. e. probably spawned on the same day. The spawning thus seems to be at its very beginning. On the Hittarp-reef near the Swedish coast opposite Helsingør egg masses (fig. 95) were observed on the following dates: $^{7}/_{7}$-41, depth 10 m, four egg masses with older embryos; $^{8}/_{7}$-41, depth 10—15 m, three egg masses; $^{15}/_{7}$-41, depth 6—8 m, two egg masses; $^{28}/_{7}$-41, depth?, four egg masses all with older embryos, and $^{3}/_{7}$-42, depth?, two egg masses at different stages of development. All the egg masses were attached to *Fucus serratus*. At Frederikshavn (N.W. Kattegat) I have seen numerous egg masses on the *Fucus*-vegetation near the low water mark as late as July and the first days of August. Thus it seems likely that the main breeding takes very small number of embryos contained in a single breeding-room as compared with the up to 900 embryos per breeding-room found near Heligoland (Linke l. c.) is also remarkable, and it seems surprising that in spite of its small production of young the stock found in the Sound is able to maintain its population. -The abnormal sinistral shells (fig. 94 B-C) are hardly of the "genetic type" known for other Gastropods, as all degrees of twisting from the normal dextral, through the planorbid, to the sinistral type may be found. Similar abnormal embryonic shells are known for instance in the North-American viviparous fresh-water prosobranch *Campeloma rufum*, which belongs to the *Viviparidae* (cf. Mattox 1935).

A stock of *Littorina saxatilis* var. *tenebrosa* taken at Lynæs harbour in the Isefjord on $^{15}/_{7}$-43, and consisting of 12 males and 16 females, showed the following conditions as to embryos in the breeding-room:

Groups of embryos contained in a single breeding-room.

Size of the female	Number of embryos in the breeding-room	Quite young embryos	Young veligers	Older veligers	Embryos in the crawling stage	Number of embryos with abnormal development
Large	505	..	×	×	×	0
—	164	×	×	..	×	Twins; 1 spm.
—	333	×	..	×	×	0
—	365	×	..	×	×	0
Medium.............	202	×	×	..	×	Twins; 1 spm.
—	135	×	..	×	×	1 shell
—	191	×	..	×	×	Twins; 1 spm.
—	98	×	..	×	×	0
—	63	×	..	×	×	0
—	214	×	×	..	×	3 shells
—	56	×	×	×	×	1 shell
—	42	×	..	×	×	0
—	0	..	..	..	..	..
—	0	..	..	..	..	..
Small	76	×	×	×	×	A few shells and twins
—	56	×	..	×	×	0

The salinity at the surface of the Isefjord is much higher and the conditions here as a whole much more marine than at the surface of the Sound. In accordance with this the Lynæs population is apparently much less degenerated than the population in the Sound. Thus at Lynæs the average number of embryos per breeding-room of females which have reached the age of reproduction is 156, i. e. $2^1/_2$ times as much as in the Sound. Four of the 12 females with embryos had a few specimens with an abnormal shell. Unfortunately, however, exact counts are not available either from the Sound or from the Isefjord, but it can be stated with certainty that the number of abnormally developing embryos in proportion to the number of normal embryos is much smaller in the Isefjord than in the Sound. — It was ascertained that the development as well as the size of the hatching young were just the same in the type-form as in var. *tenebrosa*. In the largest young found in the breeding-room (Ven, $^{20}/_{7}$-37, 4 m depth, *Zostera*) the largest diameter of the shell was 530—595 μ. The shell itself was horn-coloured with a reddish-brown columella and suture. The animals had black eyes and large or immediately after a storm. This was for instance the case on $^{1-2}/_{7}$-42 off the point of Kronborg (Helsingør). — A main series (10 vertical hauls with a standard net) taken on $^{17}/_{7}$-38 contained 7400 larvae, on $^{1}/_{8}$-38 2150 larvae, on $^{4}/_{6}$-39 4600 larvae, and on $^{25}/_{7}$-42 (off Helsingør) 5050 larvae; this means a number of 15000 to 9000 larvae in the water column over 1 sq.m of bottom, — a number far exceeding those of all other Prosobranch larvae in the Sound. The planktonic larval life seems to be rather long. Thus, the 4600 larvae from $^{4}/_{6}$-39 were all tiny and just hatched, and on $^{17}/_{6}$-39 had grown to medium-sized larvae (1100 larvae found), which on $^{3}/_{7}$-39 had reached the stage of metamorphosis and were met with in the plankton together with a new spawn of young, just hatched larvae (720 larvae found). To this may be added the 6-days' larval life spent inside the egg capsule, and it seems then probably that the individual larva will take a month or somewhat more to complete its pelagic development in the Sound. Under unfavourable conditions, however, the *Littorina*-larvae are able to prolong their pelagic larval life considerably. Plankton samples containing a considerable quantity of large larvae of *Littorina littorea* were placed in aquaria on $^{19}/_{7}$-39. When examined 6 weeks later, many of the larvae had just reached the stage of metamorphosis and had a height of the shell of 250 to 300 μ only (height of the shell at metamorphosis about 275 μ), while those kept under the most favourable aquarial conditions (surface water, large aquaria) had reached a maximum

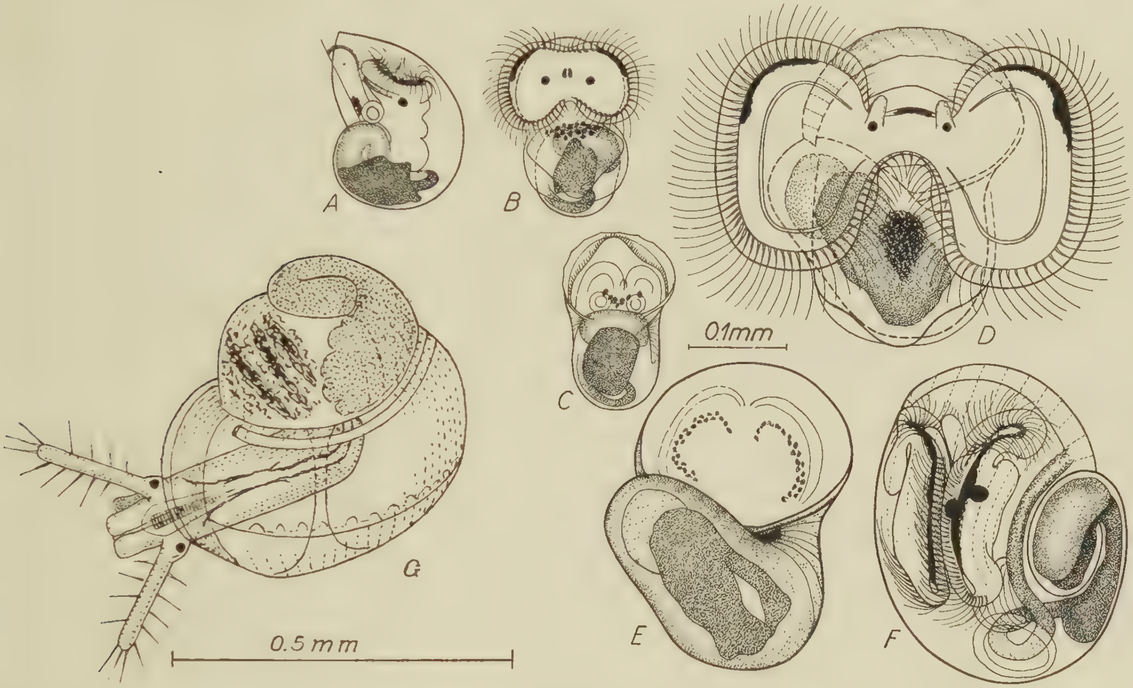


Fig. 96 A-G. *Littorina littorea* LINNÉ. — *A* to *F*. Larvae from plankton, drawn from life. *A* to *C*. Larvae in the youngest planktonic stage, seen from the left side (A), from the ventral side, swimming (B), and from the ventral side with the animal withdrawn in its shell (C). Taken in the Copenhagen South Harbour on $^{1}/_{6}$-1942 (drawn on $^{2}/_{6}$-1942). — *D* to *F*. Larvae of medium size seen from the ventral side, swimming (D) and withdrawn in its shell (E), and from the dorsal side, withdrawn (F). Off Ven, depth 18-0 m, caught and drawn on $^{5}/_{8}$-1940. — *G*. Young bottom-stage, crawling, seen from the dorsal side. The shell has a much more obtuse shape than those of *Littorina saxatilis* and *L. obtusata* in the corresponding stages. From a bottle-collector exposed off Ven, depth 16 m, from $^{19}/_{6}$ to $^{7}/_{8}$-1942. Drawn from life on the latter date.

height of the shell of 600 to 750 μ. The adaptability of the species during the pelagic life is thus very considerable. — On several occasions plankton samples were taken which contained large numbers of *Littorina*-larvae belonging to two distinct spawns, viz. large larvae just ready to metamorphose, and tiny larvae just hatched. Thus it can hardly be doubted that spawning takes place rhytmically; the relation, if any, to the lunar phases has, however, not been considered. — During September the number of larvae decreases (average 60 larvae per main series). The October average was 28 larvae per main series, and in December only a few larvae were met with in each series. The latest finds in each season were made near Ven on: $^{6}/_{1}$-38, and $^{28}/_{1}$-39, and off Helsingør on $^{19}/_{12}$-42.

The larvae (fig. 96 A—F) are very characteristic. Their shell is quite colourless with faint spiral punctations. In the younger stages the shell, 160—190 μ across, is rather flat, while the older larvae have semiglobular shells. The liver is olive-green, the stomach and intestine have black pigmentations. The black pigment of the velum on the swimming larva forms a figure resembling two eye-brows (cf. fig. 96 B—D), which, when the animal is withdrawn, are visible through the shell as too nearly parallel black lines. Further characteristics are: Black pigment on the front part of the foot (on older larvae only), yellow spots of pigment on the hindmost part of the foot close to the operculum, and two black eyes. In larvae ready to metamorphose the largest diameter of the shell is 375—390 μ and the height of the shell is 275 μ. Young bottom stages show a rapid increase in the height of the shell (fig. 96 G) and present a much more scalariform shell than the pelagic larvae.

In the Sound *Littorina* larvae are found in all layers of the water mass. Pump series from $^{27}/_{7}$-37, $^{12}/_{8}$-37, and $^{25}/_{9}$-37 show, however, that by far the majority of the larvae are met with in the uppermost part of the water column. The average content of *Littorina* larvae from the three pump series mentioned was for the uppermost 10 m 150 larvae per cubic-metre, while the water column from 10 m to 18 m (the bottom) contained only 15 larvae per cubic-metre. Thus about 90 per cent of the larvae are associated with the Baltic water layer (see further the tables on pp. 384—389).

Onoba striata (Mont.). Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. The reproduction of the species is unknown. Lebour (1934 a), however, describes from Plymouth the egg capsules of *Onoba* (*Cingula*) *semicostata*, which has a non-pelagic development. The egg capsules of this species — unlike those of other *Rissoidae* — are oval, very tough and thick-walled, without preformed exit holes, and with only one egg (240 μ across) per capsule.

B. Own remarks. Working up a large collection of *Onoba* from Iceland (Thorson 1941 a), I found that the lusitanian-boreal *Onoba striata* nearly always crowded at depths greater than 10 m, while the panarctic *Onoba aculeus* always occurred at depths smaller than 4 m. In this way their populations could be distinctly separated and will normally never overlap. In a population of *Onoba striata* taken at Tálknafjörður, N.W. Iceland, at a depth of 26 m, on $^{4}/_{7}$-1893, an egg capsule closely resembling that described by Lebour for *O. semicostata*, was found on an eroded shell of *Onoba*. The capsule (fig. 97 A—B), rather more than subhemispherical (basal diam. 550 μ, height 450 μ), had a yellowish-white surface and a structure like opaque glass. No preformed exit hole. The embryo (fig. 97 C—F) is very large (420 μ in breadth, 290 μ in height). The shell is yellowish-white in direct light, horn-coloured in transmitted light, and has one and one-fourth whorls. The large size as well as the type of the embryo show that the young hatch in the crawling stage without any pelagic life. — The whorls of the embryo found agree well with the apex of the adult *Onoba striata* (the subgenus *Onoba* has much more tumid whorls than most other *Rissoidae*). A confusion with the egg capsules of *Skeneopsis planorbis* (see below) is excluded owing to the shape of the embryo contained in this capsule, and to the fact that *Skeneopsis* is a tidal-zone dweller which is extremely rare at the depths (26 m) where the egg capsule was found.—Furthermore, in 1943—44 Mr. Erik Rasmussen found similar capsules laid by *Onoba striata* in Danish waters (the Isefjord) and was able to ascertain the non-pelagic development here also. His observations will be published later.

A rich population of the panarctic *Onoba aculeus* from Isafjörður, N.W. Iceland, taken on $^{7}/_{6}$-1895, contained five egg capsules attached to shells of living *O. aculeus*. The capsules could hardly be distinguished from those of *O. striata*, and, as in this species, they contained one single embryo each, which, however, was in dissolution. As, however, the egg capsules of *Skeneopsis planorbis* are fairly similar in shape as well as in size to those found on the *Onoba* shells, and as *Skeneopsis* was abundant in the tidal zone of Isafjörður, the capsules found may belong to *Skeneopsis*, and the problem was therefore put aside as "unsolved", until new observations from East Greenland showed that the capsules in question actually belonged to *Onoba aculeus*. A dried shell of this species from Tasiusak, East Greenland, bore an egg capsule quite similar to those from Isafjörður, and as *Skeneopsis* is totally absent from East Greenland, the identity could here be stated with certainty (cf. Thorson 1944, p. 35—36). Thus it has turned out that *Onoba striata* as well as *O. aculeus* have a non-pelagic development, the large young hatching in the crawling stage.

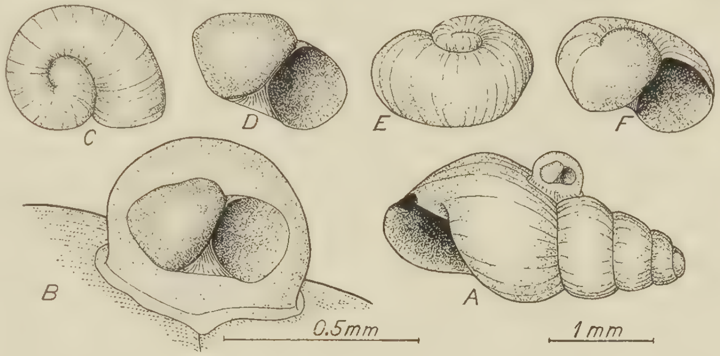


Fig. 97 A-F. *Onoba striata* (Montagu). Egg-capsule and embryos. Drawn from Icelandic specimens. See the text pp. 176—177.—*A*. Egg-capsule attached to a worn shell of *Onoba*. From Tálknafjörður, NW. Iceland, depth 26 m, on $^{4}/_{7}$-1893. (Drawn from a specimen kept in the Copenhagen museum).—*B*. The same egg-capsule with its embryo more highly magnified.—*C* to *F*. The embryo seen from above (C), the mouth (D), the dorsal side (E) and the ventro-lateral side (F).

Onoba vitrea Montagu. Hellebæk(?). Very common in south-eastern Kattegat down to Hornbæk.

Reproduction: A. Literature. Not recorded in the literature.

B. Own remarks. In our plankton samples from $^{9}/_{10}$-37 a larva was present (fig. 98 A-D) which we had never observed before. Since at first sight this larva presented only a few, not very marked characteristics, it may have been overlooked in earlier plankton series. Larvae of this type have been seen on the following dates off Ven: $^{9}/_{10}$-37 (12 spms.); $^{23}/_{10}$-37 (1 large spm.); $^{4}/_{12}$-38 (1 spm.); $^{17}/_{8}$-39 (6 spms.); $^{16}/_{9}$-39 (3 spms.), and $^{23}/_{10}$-39 (number?), and at Helsingør: $^{17}/_{9}$-41 (9 spms.); $^{7}/_{10}$-41 (6 large spms.); $^{25}/_{10}$-41 (15 large spms.); $^{11}/_{11}$-41 (3 metamorphosing spms.); $^{15}/_{5}$-42 (1 spm.); $^{17}/_{8}$-42 (7 spms.), and $^{5}/_{9}$-42 (55 spms. in all stages of development). Thus the larvae have their main season from late August to early November, being somewhat more frequent at Helsingør than near Ven.

The larva (fig. 98 A-D) has a rather flat spire. The outer lip is drawn out into a distinct beak, and the whole shell is structureless, colourless, and rather opaque. The uppermost part of the liver is yellowish, while the remaining, larger, part is reddish-brown. Apart from the liver, the two black eyes, and two tiny black spots of pigment in front of the liver, the animal is quite colourless, somewhat greyish and opaque.

A bottle-collector exposed near Ven, depth 16 m, from $^{17}/_{9}$-39 to $^{21}/_{10}$-39, contained three young bottom-stages, one of which still showed all the characteristics of the pelagic larvae described above, while the other two were more advanced in development, though they showed such a close agreement with the younger bottom stage that the whole chain could be identified as belonging to one and the same species. This agrees also well with the fact that larvae of this species were present in the plankton during the whole period in which the bottle-collector was exposed. The two oldest bottom stages (fig. 98 E-F) had a nearly globular, pale horn-coloured shell, rather shining, and with fine, dense spiral striae on the last whorl. The animals had reddish-brown livers (just as the pelagic larvae), two black eyes, a few yellow spots of pigment on the head, but were otherwise whitish-colourless. Two long slender tentacles, an operculum, and a distinct umbilicus were seen. — I succeeded in dissecting out the radula of the largest of the three bottom stages and could ascertain that the radula was of the *Onoba*-type. At first,

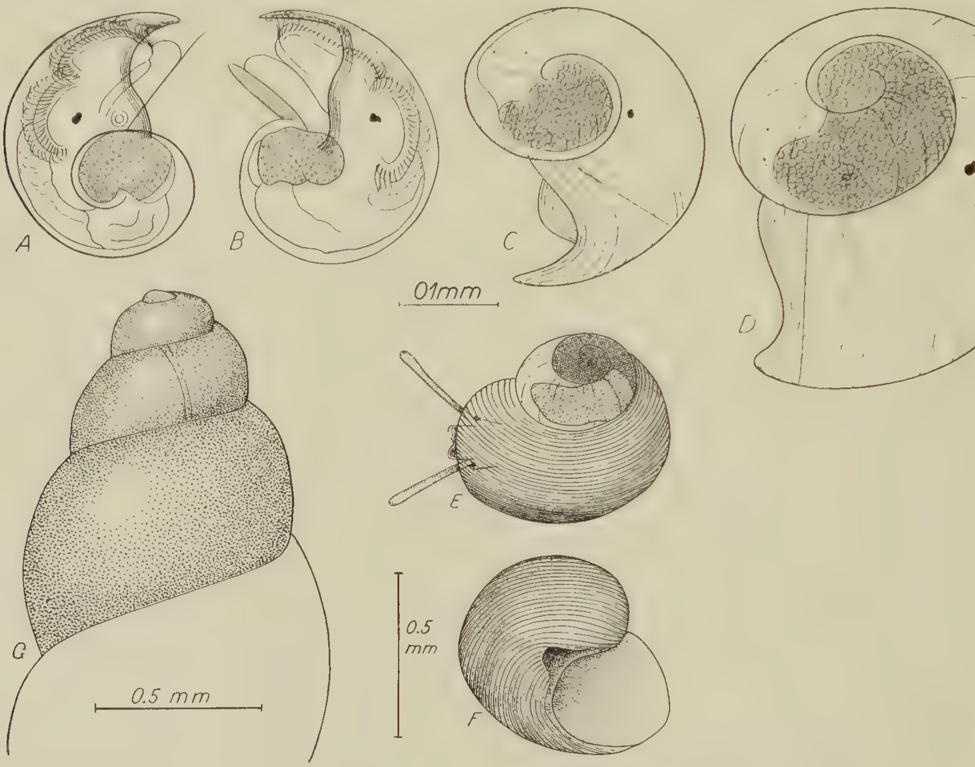


Fig. 98 A-G. *Onoba vitrea* Montagu. *A* and *B*. Larvae of medium size from plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{5}/_{9}$-1942 (drawn from life on $^{6}/_{9}$). Seen from the right (A) and the left (B) side. — *C*. Somewhat older larva in lateral view. From plankton off Ven, depth 18-0 m, caught and drawn living on $^{9}{}_{10}$-1937. — *D*. Late larva in lateral view. From the same locality, depth and date as Fig. C. — *E* and *F*. Young bottom stage seen from the dorsal side, crawling (E) and from the ventral side, withdrawn in its shell (F). From a bottle-collector exposed off Ven, depth 16 m, from $^{17}/_{9}$ to $^{21}/_{10}$-1939 (drawn from life on the latter date; see the text pp. 178—179). — *G*. Apex of adult specimen (the shell is somewhat worn, therefore no spiral striae). Taken off Frederikshavn (from a specimen in the Copenhagen museum).

therefore, I referred the larva in question to *Onoba striata*, but as this species later on proved to have a non-pelagic development (see above), the only other species that might come into consideration was *Onoba vitrea*, adults of which are common immediately north of the area investigated. The apex of this species (fig. 98 G) has the same size and the same obtuse shape as the oldest bottom stages from the bottle-collector, but on all the adults from Danish waters the periostracum on the apex had been worn off, so that the structure was not visible. Jeffreys (1867, p. 40), however, describes the shell of this species as semitransparent, of a glassy lustre: "... under microscope ... the surface exhibits extremely fine regular and close-set spiral striae". Thus the identity of the larva seems to be beyond all doubt: the radula was that of an *Onoba*. *Onoba vitrea* is the only species of *Onoba* in the Sound the development of which is unknown. The newly metamorphosed young agrees in size and shape with the apex of *Onoba vitrea*, and the young as well as the adult *O. vitrea* have semitransparent, glassy shells with regular, close-set spiral striae. Hence, I have no hesitation in referring the larvae found to *Onoba vitrea*.

Alvania punctura (Montagu). Adult specimens not known from the Sound, but from southern Kattegat.

Reproduction: A. Literature. Lebour (1934a, 1937) has described and figured the eggs and larvae. Egg capsules laid in the laboratory on the shells of the parents are lens-shaped to more than semiglobular, thick-walled and small (320—480 μ across), and each capsule contains 12—14 eggs (60 μ across). No larvae were hatched, but larvae from plankton were reared to the adult stage. Young larvae with one and a half whorls are "sculptured with spiral striae and dots in between, similar to that of *Rissoa sarsi*, but smaller. Beyond the first whorl and a half there are small raised spots on the whorls, by which it can be distinguished at once from *R. sarsi*. The animal is yellowish-white and the velum is colourless, the shell becoming dark horn colour". "Larval shell about to metamorphose 0.64 mm long".

B. Own remarks. Very characteristic larvae agreeing with the descriptions and drawings of Lebour are commonly met with in the Sound plankton, where they may only be confused with larvae of *Rissoa sarsi* and with larvae probably belonging to *Alvania abyssicola* (see this species). In most cases it was possible to state their exact identity, but it cannot be excluded that the larvae of *Alvania punctura* and *A. abyssicola* have been confused on certain occassions. Larvae of *Alvania punctura* were met with in the Sound on the following dates (a ? in the paranthesis after the date means that confusion with larvae of *A. abyssicola* may have taken place); off Ven: $^{17\text{-}19}/_{10}$-36 (1 spm.); $^{27}/_{7}$-37 (1 spm.); $^{4}/_{9}$-37 (?, 1 large spm.); $^{12}/_{9}$-37 (1 spm.); $^{25}/_{9}$-37 (1 large spm.); $^{23}/_{10}$-37 (1 large spm.); $^{6}/_{1}$-38 (3 spms.); $^{13}/_{8}$-38 (?, 3 large spms.); $^{26}/_{8}$-38 (?, 1 large spm.); $^{24}/_{9}$-38 (?, 2 spms.); $^{8}/_{10}$-38 (?, 1 spm.); $^{16}/_{9}$-39 (?, 7 large spms.), and off Helsingør: $^{17}/_{9}$-41 (1 large spm.); $^{25}/_{10}$-41 (1 large spm.); $^{6}/_{7}$-42 (?, 21 large spms.); $^{18}/_{7}$-42 (13 spms.); $^{17}/_{8}$-42 (11 large spms.), and $^{5}/_{9}$-42 (4 large spms.); the larvae thus occur in the late summer and autumn.

The larvae (fig. 99 A-C) agree in all details with those described by Lebour (l. c.). The first whorl is yellowish, horn-coloured, and sculptured with spiral striae consisting of small dots, the reddish-brown liver showing through the shell. The next two whorls are colourless and have a structure consisting of numerous tiny vesicles on the surface, which are replaced by oblique striae and by a few faint spiral lines round the periphery. The outer lip has a rather pronounced beak; two large black eyes are seen through the shell. Apart from dark-purple pigment on the foot the animal is quite colourless. The largest plankton stage found had a maximum height of the shell of about 450 μ. — The larva fig. 99 D from Gullmarfjord plankton (Bohuslän, Swedish W.coast), which seems to belong to the same species (the adults are common in the area in question), is very near the stage of metamorphosis and has a rather solid last whorl with the first faint traces of the adult structure. Dark-purple pigment is seen in the middle of the foot and near the lower end of the columella, and the foot has several dots of lemon-coloured pigment. The shape of this Gullmarfjord-larva agrees fairly well with

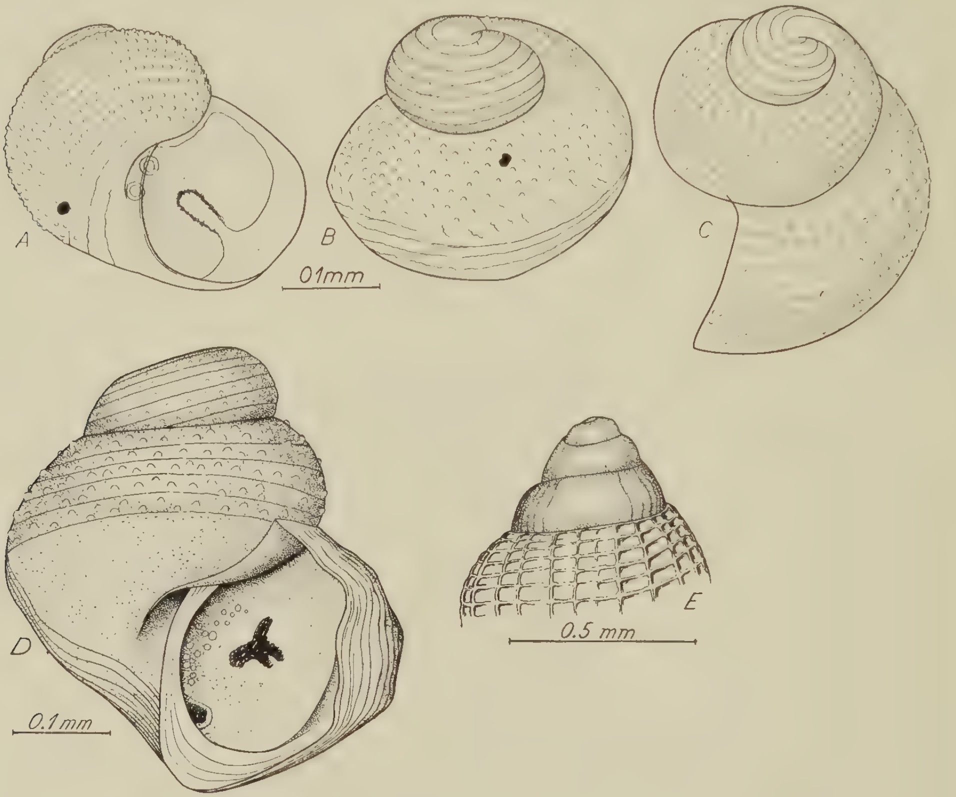


Fig. 99 A-E. *Alvania punctura* (Montagu). Larvae from plankton off Ven, depth 18-0 m. — *A* and *B*. Larvae of medium size, seen from the ventral side (A) and from the dorsal side (B) (drawn from life on $^{17-19}/_{10}$-1936). — *C*. Oldest planktonic stage found. Taken in a living condition on $^{27}/_{7}$-1937 (drawn dead on $^{1}/_{8}$-1937). — *D*. Old larva from Gullmarfjord plankton (Bohuslän, Swedish W.coast), depth 30-0 m, drawn living on $^{25}/_{8}$-1945. Seen from the ventral side. Near the stage of metamorphosis. — *E*. Apex of adult specimen (somewhat worn) taken near Schultz Ground (S. Kattegat), depth 28 m (from a specimen in the Copenhagen museum).

that of the (somewhat worn) apex of an adult *A. punctura* from the Copenhagen museum (fig. 99 E). — Metamorphosed stages were not observed.

While the larvae referred here to *Alvania abyssicola* are often met with in the Sound in quite young stages (1$^1/_2$ whorls), those of *Alvania punctura* are normally met with in older stages only, — a fact which is in good agreement with the distribution of the adults of both species. *Alvania punctura* is not known in the adult stage from the Sound, and the larvae found — all of them older — had probably drifted to the Sound from the Kattegat. *Alvania abyssicola*, however, is very common in the northern part of the Sound, and accordingly the larvae referred here to this species are often young and just hatched, i. e. spawned in the Sound itself.

Alvania abyssicola Forbes (= **A. subsoluta** (Aradas)). Rather common at fairly great depths in the northernmost part of the Sound.

Reproduction: A. Literature. The larva of this species has so far been unknown. Lebour, however, (1934 a, pl. IV, figs. 8—10) describes a larva, which "is so much like *Rissoa sarsii* and *Alvania punctura* that there is probably some relationship". Its most characteristic feature is the apex, which has spiral striae divided up by lines. "After $1^{1}/_{2}$ whorls the structure is irregular dot-like markings in a few lines round the periphery, animal pale yellowish with large colourless velum". This larva was later identified with *Alvania crassa* (Lebour 1936).

B. Own remarks. From the Sound larvae are at hand which in several respects resemble those described by Lebour. Our larvae (fig. 100 A-C) show such close similarities to those of *A. punctura* that a high magnification is necessary to distinguish them. When sufficiently magnified, however, they are easily distinguishable from the latter as a distinct species. The horn-coloured apex, which has an oblique position as compared with the following whorls, is very beautiful with spiral zigzag lines connected with regular transverse lines to a precise pattern. The following whorl is colourless and has a beak on the outer lip, which had a faint keel like that of *A. punctura* and may or may not have small vesicles like this latter species (fig. 100 C has vesicles, fig. 100 B has none). The liver is yellowish-brown, showing through the shell, but apart from this the whole animal is colourless. Two black eyes and distinct statocysts were seen; the animal closely resembles that of *A. punctura*. The youngest larvae found measured 210—220 μ across their shells, the oldest ones 320 to 330 μ. — Accordingly the parents should most likely be sought for within the genus *Alvania*, as the larvae found are very similar to those of *A. punctura* and *A. crassa*, though not belonging to either of them. *A. crassa* is altogether unknown from the Danish seas. *Alvania abyssicola* is the only species within this genus which is known in adult animals from the Sound itself, where it is rather common. The apex of the species examined in adult shells (fig. 100 D) was oblique as compared with the following whorls and was provided with spiral striae, between which a few transverse lines could be distinguished. No regular pattern like that found in the larva was present, but these very delicate transverse lines probably have been worn off in all the adult shells. Thus it seems very likely that the larvae described above should be referred to *Alvania abyssicola*.

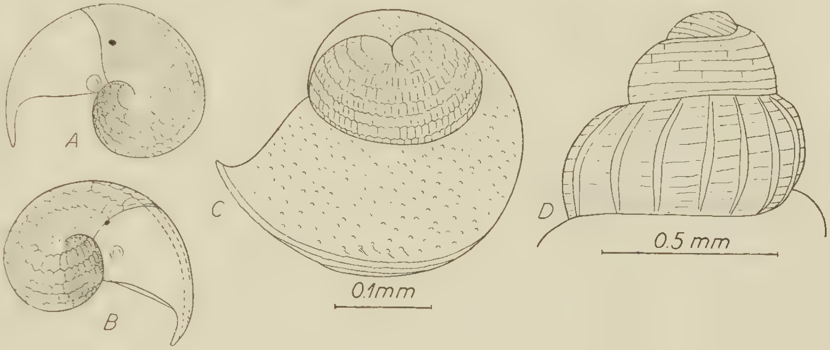


Fig. 100 A-D. *Alvania abyssicola* Forbes. — *A* to *C*. Larvae from plankton off Ven, depth 18-0 m, drawn from life on the day of capture. — *A*. Young larva seen from the left side. — *B*. The same from the right side, showing the oblique-spiral shape of the first whorl ($^{1}/_{11}$-1936). — *C*. Old larva seen from the dorso-lateral side ($^{15}/_{11}$-1936). — *D*. Apex of adult specimen taken SSW. of the Faroes, depth 398 to 425 m.

Larvae of this type were taken off Ven on: $^{1}/_{11}$-36 (2 spms.); $^{14}/_{11}$-36 (3 spms.); $^{4}/_{9}$-37 (1 spm.); $^{24}/_{9}$-37 (3 older spms.), and off Helsingør on: $^{20}/_{6}$-42 (2 spms.); $^{17}/_{8}$-42 (4 spms.), and $^{5}/_{9}$-42 (6 quite young and 2 older spms.) (see further the dates for larvae of *A. punctura*). The main season is thus the same as for the larvae of *A. punctura*, viz. the late summer and autumn. Most of the larvae found are small, i. e. spawned in the Sound itself. Metamorphosing stages were not seen.

Rissoa sarsi Lovén. Distribution insufficiently known; see below.

Reproduction: A. Literature. The eggs and larvae are figured and described by Lebour (1934a, 1935c, 1936, 1937a). The lense-shaped egg capsules of the typical Rissoid form are 480 μ across (pelagic capsules at first referred to this species belong to *Littorina neritoides*), colourless, thick-walled, and contain 10—14 eggs, each egg about 90 μ across. The just hatched larva, 120 μ across, has a shell with spiral striae and dots in between closely resembling that of *Alvania punctura*. But "beyond the first whorl and a half the upper part of the shell is smooth, the periphery and just below having rows of interrupted striae", while the corresponding whorl in *Alvania* is provided with numerous small vesicles (see this). "Animal yellowish, in older larvae with dark brownish-purple pigment at the base of the foot . . .". Velum at first colourless, later with a fine, dark band. Shell on metamorphosis 480 μ in height, with $2^1/_2$—3 whorls. Larvae kept in the laboratory grew into adults.

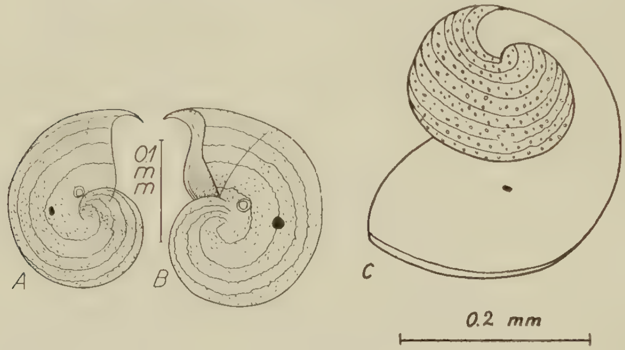


Fig. 101 A-C. *Rissoa sarsi* Lovén. Larvae from plankton off Ven, depth 18 to 0 m.—*A* and *B*. Young larvae caught on $^{25}/_{3}$-1939, drawn from life on $^{26}/_{3}$-1939. Seen from the right side (A) and from the left side (B).—*C*. Old larva, caught and drawn from life on $^{4}/_{4}$-1937 (sketch by Erik Smidt); seen from the right side.

B. Own remarks. While larvae of *A. punctura* and *A. abyssicola* had their maximum occurrence in the late summer and autumn, larvae were present in spring plankton in larger numbers, which, though resembling them in several respects, were different in having a distinct brownish-black velar pigment and no vesicles on that part of the shell which is just below the spirally striated apex. These characteristics agree with those given by Lebour for larvae of *Rissoa sarsi*, and if we compare our figure 101 C with that given by Lebour (1934a, pl. I fig. 14), we shall find such a close agreement that their identity may hardly be questioned.—Petersen (1888) mentions the difficulties of distinguishing adult shells of *Rissoa sarsi* and *R. inconspicua* in Danish waters, but is of opinion that *R. sarsi* is to be found in the Kattegat as well as in the Belts. In the Copenhagen museum there are several specimens of *R. sarsi* from the Sound, but so far I have been unable to find spiral striae on their apices. These fine striae may, however, easily be worn off in adult shells.

Larvae of this type (fig. 101 A-C) were taken off Ven on: $^{4}/_{4}$-37 (1 spm.); $^{18}/_{4}$-37 (1 spm.); $^{2}/_{5}$-37 (1 spm.); $^{23}/_{5}$-37 (2 spms.); $^{3}/_{4}$-38 (6 spms.); $^{18}/_{4}$-38 (55 spms. in all sizes); $^{10}/_{5}$-38 (26 spms., most of them older larvae); $^{25}/_{5}$-38 (6 large spms.); $^{6}/_{6}$-38 (6 large spms.); $^{10}/_{4}$-39 (1 spm.); $^{17}/_{5}$-39 (2 spms.); $^{4}/_{6}$-39 (1 spm.); $^{15}/_{7}$-39 (5 spms.), and off Helsingør on: $^{10}/_{4}$-42 (13 young spms.), and $^{4}/_{6}$-42 (9 spms.). The main occurrence is thus from April to July with a maximum in April-May. Several of the larvae found are quite small, just hatched, and seem to originate from the Sound itself.

Rissoa inconspicua Alder. Throughout the Sound, rather common.

Reproduction: A. Literature. Egg capsules figured by Meyer & Möbius (1872), and egg capsules and larvae described and figured by Lebour (1934a, 1937a), who gives the following data: Egg capsules of the common Rissoid form, 480—640 μ across, contain about 6—9 eggs, 80 μ across. "Young hatch as veligers in 10 days; shell smooth, unsculptured, about

0.10 mm across; velum colourless at first, about 0.10 mm across; foot, eyes, otocysts and tentacles all present. Velum later bordered with brown; older larvae with two faint spiral lines round body whorl". Newly metamorphosed shell with purple apex. "No sculpture on the first three whorls except a slight spiral broken line just above the periphery of third whorl". Common near Plymouth in early autumn.

B. Own remarks. The description and figures of Lebour provide only a slight basis for the identification of this larva in plankton. Only the newly hatched larva is figured (resembling several other young larvae). The purple apex of nearly metamorphosed shells seems, however, to indicate that older planktonic larvae have yellowish-brown, horn-coloured, shells — not colourless transparent shells as for instance *Littorina* and *Nassa*. The adults, which live at rather small depths in the Sound, according to all experience spawn in summer, and as the adults are rather common, the larvae may be supposed to be frequent in the plankton. We thus have to look for larvae with yellowish-brown shells, which occur fairly frequently in the summer plankton.

Larvae of this type (fig. 102) were taken off Ven on: $^{6}/_{6}$-37 (about 40 spms.); $^{1}/_{7}$-38 (about 70 spms.); $^{17}/_{7}$-38 (375 spms.); $^{1}/_{8}$-38 (165 spms.); $^{15}/_{7}$-39 (7 spms.); $^{5}/_{8}$-39 (about 15 spms.); $^{18}/_{8}$-39 (10 spms.), and $^{16}/_{9}$-39 (56 spms., in swimming-crawling stage), and off Helsingør on: $^{17}/_{9}$-41 (11 large spms.); $^{7}/_{10}$-41 (7 large spms.); $^{11}/_{11}$-41 (1 spm.); $^{6}/_{7}$-42 (13 spms.); $^{18}/_{7}$-42 (4 spms.), and $^{25}/_{7}$-42 (about 90 spms.). The main season is thus from June to late September, and, in agreement with this, bottle-collectors exposed near Ven at a depth of 16 m from $^{17}/_{9}$ to $^{21}/_{10}$-39 and from $^{19}/_{6}$ to $^{7}/_{8}$-42 contained numerous young bottom stages of *Rissoa inconspicua*. No other larvae common in the plankton within that period could with the slightest probability be referred to *Rissoa inconspicua*, and these facts seem to support the identification given above.

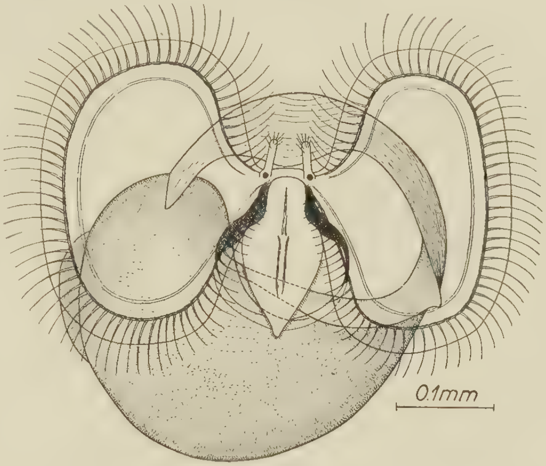


Fig. 102. *Rissoa inconspicua* Alder. Larva in "swimming-crawling stage". From plankton off Ven, depth 18-0 m, caught and drawn from life on $^{19}/_{8}$-1944.

Rissoa membranacea (J. Adams). Usually common in *Zostera* meadows throughout the Sound, but from 1939 reduced considerably in number during the *Zostera* epidemic.

Reproduction: A. Literature. Meyer & Möbius (1872), Fischer (1892), and Lebour (1934 a, 1937 a) describe and figure the egg capsules and the larvae of this species, but, as was the case with the preceding species, the larval figures are not detailed enough to allow of a safe identification. Erik Smidt (1938), however, has published his studies on the breeding biology of this species from the Sound and has figured eggs and larvae. His investigations, carried out from the Ven laboratory, form part of the present survey and will be briefly summarised here: Lens-shaped egg capsules, about 800 μ across, are attached to leaves of *Zostera*. Newly hatched larvae (175 μ across the shell) have a faintly yellowish shell with fine wavy spiral lines and a shell-tooth at the mouth. Velum bilobed, with a faint brownish pigment string at the margin. Liver yellowish-brown; eyes and statocysts distinct. Older planktonic larvae are characterised as follows: "The typical plankton-stages have a yellowish shining shell with shell tooth. On the upmost whorl the spiral sculpture may sometimes be faintly visible. Velum consists of two round lobes, the right being often a little larger than the left; along the edge is seen a thin, brown pigment string, and at direct light a quantity of yellow pigment is seen both on foot and proboscis". Older larvae have also black pigment on the foot.

Pelagic larvae are abundant among *Zostera*-leaves in the Sound from the middle of June to the end of July, but are of no importance in the "high sea plankton". Only when a gale makes the sea rough, will large numbers of larvae be carried away from the *Zostera*-meadows by the heavy swell to the plankton of the open sea. Metamorphosed young specimens settle in large numbers in August and reach their adult shape and size as early as September.

B. Own remarks. Simultaneously with the *Zostera* epidemic, which since 1938—39 has destroyed the whole vegetation in the Sound, the adults as well as the larvae of *R. membranacea* have nearly disappeared and are now very rare.

Hydrobia ulvae PENNANT. Throughout the Sound, extremely common, especially in the *Abra* community.

Reproduction: A. Literature. MIRIAM ROTHSCHILD (1940) states that the veligers, which hatch 10 days after fertilisation, are very difficult to rear in captivity. The same author (1936, 1941) found that infections of larval trematodes locally may sterilise a large percentage of the populations of this species. Such sterilised specimens will grow to a gigantic size. MEYER & MÖBIUS (1872), HERDMAN (1888), QUICK (1920), and LEBOUR (1937 a) describe and figure the egg capsules, and HENKING (1894) gives a detailed description with figures of egg capsules and larvae from the mouth of the Ems. The results of HENKING and LEBOUR may be summarised as follows: Egg capsules, 600 μ across, surrounded by sand grains and attached to the shells of the adults contain from three to twelve (or even twenty-five (QUICK 1920)) eggs floating in an albuminous fluid. The newly hatched larva has a colourless to faintly greenish shell of about one and a half whorls, with tentacles, eyes, otocysts, foot, and operculum. The eyes are black; on each velar lobe is a semilunar, reddish-black string of pigment. The hindmost part of the intestine has a black pigmentation. HENKING (l. c. pl. 4, fig. 18) figures an older larva of *Hydrobia* from Sylt, and states that "in larger larvae I have seen the radula characteristic of *Hydrobia*, which had already formed", and "I have seen faint longitudinal striae running parallel to the whorls in the last whorl of the larval shell. The striae are rather far apart and resemble the striae of an object micrometer when highly magnified" (translated from the German). MEYER & MÖBIUS (l. c.) mention from Kiel from September larvae, 200—400 μ long, swimming at the surface, which could be referred by their radulas to *Hydrobia ulvae*. HENKING (l. c.) mentions adult animals taken in large numbers with a plankton-net when the sea was rough. PELSENEER (1926 b) states that the females of three populations constitute 58, 68, and 69 per cent respectively.

B. Own remarks. Adult specimens of *Hydrobia* with egg capsules attached to their shells (fig. 103 A-B) occur in the harbour of Copenhagen in early May, and intense breeding takes place here and in the Sound itself during the whole summer, at least until July or August. Breeding was also observed at Frederikshavn (N.W. Kattegat) in August. The uncleaved egg is about 90 μ in diameter.—*H. ulvae* is undoubtedly the commonest Prosobranch within the Sound and occurs at all depths from the shore to about 20 m. On the mixed bottom (*Abra* community), between depths of 8 and 20 m, more than 1000 specimens per sq.m may often be found, all of which have egg capsules on their shells during the summer. If, therefore, the pelagic larval stage were of long duration, larvae of this species might be

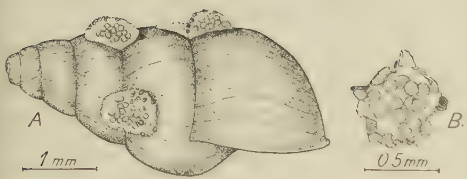


Fig. 103 A-B. *Hydrobia ulvae* Pennant. — *A*. Adult female with three egg-masses attached to its shell. — *B*. One of the egg-masses seen from below. Caught in the Copenhagen South Harbour and drawn from life on $^{25}/_{4}$-1944.

supposed to play a totally dominant rôle within the larval stock of the Sound. This, however, is not the case. — In the southern harbour of Copenhagen *Hybrobia ulvae* is still more dominant than in the Sound proper, covering the bottom in large quantities. Larvae from egg capsules (fig. 104 A—C) taken here hatched on $^{27}/_{5}$-42. On $^{1}/_{6}$-42, i. e. at least one month after the beginning of the breeding-season, a series of plankton hauls were taken in the same locality to secure pelagic larvae of *H. ulvae* in all stages. Large numbers of larvae were found and easily identified with *H. ulvae*, but they were all of the same size, viz. that found for larvae in the hatching stage. These larvae (fig. 104 D—F), which agreed well with Henking's figs. 14—15, were 150—170 μ across the faintly horn-coloured shell, which had one whorl only. Semilunar purplish-black pigment on the velum ("eyebrows") and round the mouth; two black eyes and a black-pigmented hindmost part of the intestine are distinct. Large otocysts; yellowish-grey liver. The shell had no beak at the mouth, and the velum was very small, hardly bilobed (fig. 104 D), features which point to a very short pelagic larval life. As, furthermore, no larger larvae were seen among the numerous planktonic larvae after at least one month of breeding, and as none of the larger larval forms from the Sound can be referred to this species, it seems justifiable to conclude that their pelagic life is very short, and that the larvae grow inconsiderably during this stage. A shortened pelagic life of this species was already suggested by Lebour (1937 a, p. 113). — The older larvae mentioned and figured by Henking from Sylt (see above) should be referred to another species, probably *Littorina littorea* (the pigmentation as well as the spiral striae on the shell support this conjecture). The older larvae, which according to Meyer & Möbius float in the water, and which show the radula characteristic of *Hydrobia ulvae*, are not planktonic, but are whirled up from the bottom by the rough sea.

After having studied the larvae thoroughly in the Copenhagen harbour in May-June 1942, I succeeded in finding a single young larva in a main series off Helsingor on $^{20}/_{6}$-42, and it can be taken for granted that in the previous years some of these small larvae have been listed as "small larvae of Prosobranch sp.". But even when this possibility is taken into consideration, these larvae are so rare that they play no part at all in the plankton in the Sound. Probably the larva takes little or no food at all from the water during its short pelagic life. — In a material collected by Erik Rasmussen at Vellerup Vig, the Isefjord, on $^{25}/_{5}$-43, larvae of *Hydrobia ulvae* were abundant, and on $^{5}/_{6}$-43 several egg masses with young eggs were observed by the present author in the middle part of Isefjord. — The larvae are photopositive.

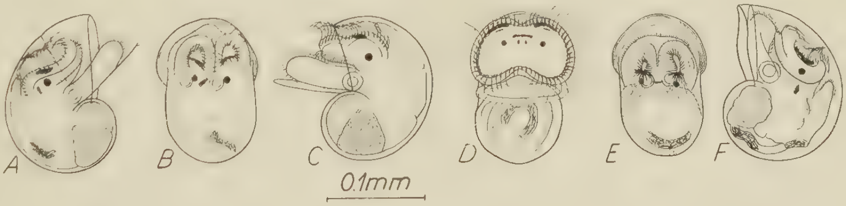


Fig. 104 A-F. *Hydrobia ulvae* Pennant. Planktonic larvae. — *A* to *C*. Larvae hatched in aquarium on $^{27}/_{5}$-1942 (drawn from life on $^{28}/_{5}$-1942) from egg-masses taken in the Copenhagen South-Harbour, seen from the right side (A), the dorsal side (B), and the left side (C). — *D* to *F*. Oldest larvae found in plankton from the South Harbour, drawn from life on $^{2}/_{5}$-1942, seen from the ventral side, swimming (D), from the dorsal side (E), and from the left side (F). A comparison between figs. *A* to *C* and *D* to *F* shows that slight growth only or no growth at all takes place in the pelagic stage.

Hydrobia ventrosa (Montagu). Southern part of the Sound (Saltholm, Copenhagen harbour), common.

Reproduction: A. Literature. Quick (1920) and Robson (1922) have described the anatomy of the species. Van Benthem Jutting (1922, p. 405, 1933) has described and figured the egg capsule (as *Hydrobia stagnalis*), and her figure has been reproduced by Ankel (1936 a). The capsules, 260 μ across, are globular, surrounded by grains of sand. Each egg capsule contains a single egg or embryo, which leaves the capsule in a crawling stage with a shell of $1^1/_4$ whorls, 175 μ across. What Lebour (1937 a) mentions as *Hydrobia ventrosa*, is *H. jenkinsi* (see this species).

B. Own remarks. The reproduction in the Sound agrees in all particulars with that mentioned above. The egg capsules from Saltholm (fig. 105 A—C, kindly placed at my disponal by Mag. sc. G. Mandahl-Barth) as well as those from the Copenhagen harbour are attached to stones or to the shells of this species; each capsule contains one egg only, and the embryos (fig. 105 B—C) always hatch in the crawling stage without any pelagic life. The breeding season is rather long. Egg capsules were observed during the period from early May to July.

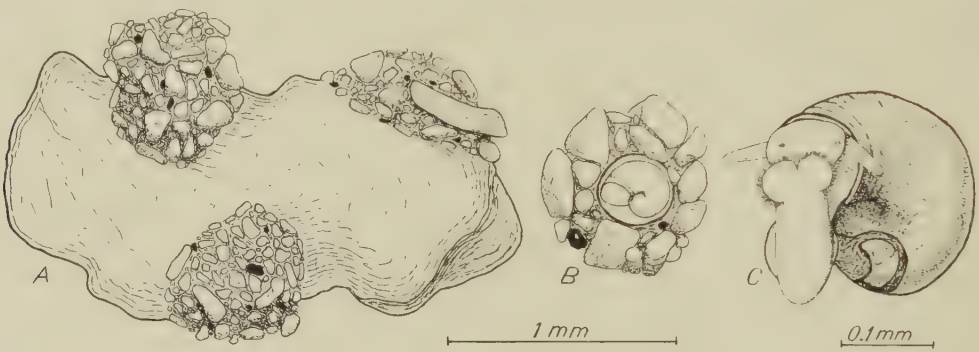


Fig. 105 A-C. *Hydrobia ventrosa* (Montagu). — *A*. Three egg-masses attached to a stone. From the shore of Saltholm. — *B*. A single egg mass with its large embryo, seen from the under surface after having been removed from its substratum. From Randers Fjord, E. Jutland. — *C*. Late embryo nearly ready to hatch with the velum partially reduced. From the shore of Saltholm. — The sketches are drawn and kindly placed at my disposal by Mag. sc. G. Mandahl-Barth.

Hydrobia (Potamopyrgus) jenkinsi Smith. Known from Gråen near Landskrona, and from the south harbour of Copenhagen; common locally.

Reproduction: A. Literature. Taylor (1900), Oldham (1901), Boycott (1917, 1919), Quick (1920), and Rothschild (1940) have studied the reproduction of this species. Finally, Robson (1920, 1923, 1926) discusses the results of these authors and adds a few detailed observations on the reproduction of *H. jenkinsi*. The data given by these authors may be summarised as follows: This is the only molluscan species hitherto known with certainty to be parthenogenetic. Males are unknown, and not the slightest traces of sperms were found in the several hundred specimens examined. The adults, which may have one or two breeding seasons a year, and which probably breed in other localities all the year round, are viviparous. A full-grown female normally contains 35—45 young in its "brood-pouch" at the same time. These embryos are in all stages of development. They are surrounded by an egg membrane, which contains a nutritive (?) fluid. The oldest embryos in the brood-pouch have already broken through the egg membrane. They hatch as young in the crawling stage. Young hatched in the spring will probably reach maturity in the same year. A young specimen, 1 mm long, isolated on $^{28}/_{6}$-19, on $^{12}/_{9}$-19 contained thirty embryos, while three of its young had already hatched. The young are easily reared in captivity. Ankel (1936a, p. 180, fig. 177) figures the adult female with embryos in the brood-pouch. Krull (1935) found that a population kept by him for a long time in an aquarium proved to consist of hermaphrodites, and he is of opinion that self-fertilisation takes place.

B. Own remarks. During a visit to Ringkøbing Fjord (W. Jutland) on $^{9\text{-}10}/_{6}$-43, I found that *Hydrobia jenkinsi* was very frequent at a depth of 1 to 2 m. Hence, I took the opportunity to examine a couple of specimens. All specimens found contained eggs in the brood-pouch. Fig. 106A shows an adult female the shell of which has been removed. The soft parts contained in the shell are dark-pigmented, with a white ovary and a brown liver showing through the body wall. The brood-pouch — a large sac on the dorsal side behind the head — is quite distended by embryos, which are distinctly seen through the body wall as well as through the shell. The greyish-white mantle-border, which contrasts with the black-pigmented mantle wall behind and the blackish slate-grey head in front, lies rather close to the head, and forms the anterior limit of the brood-pouch. The yellowish-brown hindmost part of the foot with the operculum is seen below. — The embryos in the brood-pouch of *H. jenkinsi* are not divided into such distinct groups representing different stages of development as are known for *Littorina saxatilis* (see this, pp. 170–172). Fig. 106 B–H shows embryos in different stages of development from the quite undeveloped egg (185—190 μ across) to the crawling stage, — all originating from a single brood-pouch. In accordance with this it may be supposed that eggs are spawned singly in the brood-pouch at certain intervals. Observations made in glass-dishes have further proved that the young hatch singly, not in crowds. – The number of eggs and embryos in the brood-pouch of 20 females examined at Ringkøbing were: 5; 7; 8; 9; 15; 18; 19; 20; 21; 22; 23; 23; 24; 26; 27; 30; 30; 31; 31, and 36 respectively, i. e. about 22 embryos, on an average, per brood-pouch, which is a smaller number than is known from England, and a much smaller number than is known from the brood-pouch of *Littorina saxatilis*. The young hatch in the crawling stage with yellowish, horn-coloured shells, 400—410 μ across, with a much reduced velum, two black eyes, and two large tentacles with large cilia on their tips.

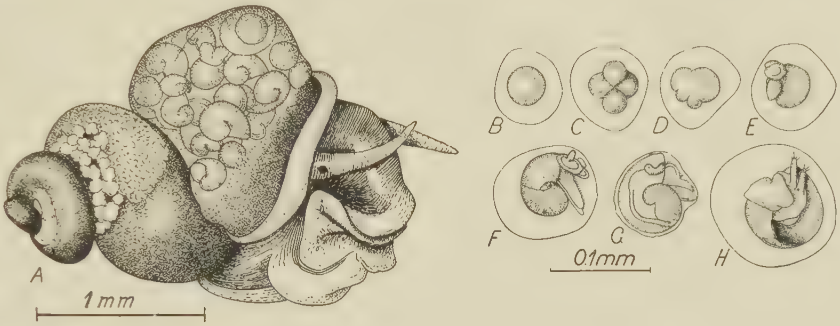


Fig. 106 A-H. *Hydrobia jenkinsi* Smith. From Ringkobing Fjord, W. Jutland, depth $1^{1}/_{2}$ m, caught on $^{9}/_{6}$-1943 (drawn from life on $^{10}/_{6}$-43). — *A.* Adult female with the shell removed to show the brood-pouch with the embryos. — *B* to *H.* Eggs and embryos contained simultaneously in a single brood-pouch. Embryos of all sizes occur among each other unlike the conditions in *Littorina saxatilis* (cf. fig. 94 E-G).

Specimens from the Sound (Copenhagen harbour and Landskrona) seem to reproduce in precisely the same way as those from Ringkobing Fjord. The brood-pouch was filled with embryos of every size in winter (January: at Landskrona and Copenhagen) as well as in summer (Copenhagen), and breeding seems thus to take place all the year round. Erik Smidt (1944) has observed that the young, which normally hatch in the crawling stage, may hatch with a very small, but active velum, and they have, then, a short pelagic "floating stage", until the velum is totally reduced. Although looking for them, I never found hermaphroditic specimens. They may have been overlooked, but as many careful scientists have failed to observe them in large populations it is quite possible that some populations are parthenogenetic, some hermaphroditic. This seems to agree well with ANN SANDERSON's (1939) statement of a diploid chromosome number of 36 to 44 in Scottish specimens, while RHEIN (1935) found the diploid chromosome number to be 20 to 22, i. e. half the number found in a population from the European continent.

Homalogyra atomus (PHILIPPI). Throughout the Sound on soft bottom: Copenhagen, Taarbæk, Ven, but probably often overlooked.

Reproduction: A. Literature. JEFFREYS (1867) mentions dried up spawn capsules found inside the upper cavity of the last whorl, and LEBOUR (1937 a) adds, that "Capsules have been seen in the same position as that described by JEFFREYS, but they were much smaller. It is probable that these were the egg capsules, but they have not been hatched out. The young probably hatch in the crawling stage, for crawling young with shells only 0.16 mm across have been seen; it is almost certain that there are no free-swimming stages. The young are found throughout the year".

B. Own remarks. Nothing is known about the reproduction in the Sound. In the rather large material of this species (preserved in alcohol) from East Greenland, West Greenland, Iceland, and the Faroes, kept in the Copenhagen museum, I have only found a single specimen with capsules like those described by JEFFREYS (l. c.) and figured by LEBOUR (1937 a, fig. 2 b). Thus, 29 adults from East Greenland preserved in alcohol and captured in quite shallow water in July, i. e. the month with optimal temperatures in which the other shallow water animals are known to spawn, contained not the slightest traces of egg capsules in their last whorls. On the outer surface of the shells of two animals, however, some very small capsules were found which closely resembled the capsules known from Rissoans, Skeneopsis, etc., but they were smaller. These capsules had probably been laid by *Homalogyra*, but the problem is still unsolved (cf. THORSON 1944, pp. 39—40).

Turritella communis RISSO. Northern and middle parts of the Sound, rather common locally.

Reproduction: A. Literature. LEBOUR (1933 a) has described and figured the eggs and larvae from Plymouth. Natural breeding season apparently from April to July. Small pink eggs, 100 μ across, in a number of 6—20 are deposited in a globular capsule, 640—1120 μ across, and some hundreds of capsules may be collected in large clusters, 6—10 mm across, of a pinkish-brown to yellowish colour. All the eggs develop and the larvae hatch 8—10 days after the spawn has been shed. The newly hatched larva is colourless; the transparent, unsculptured shell, 160 μ across, has only one whorl, "the outer lip is hardly drawn out into a tooth". Velum, 180 μ across, is colourless, tentacles short and blunt, eyes and otocysts conspicuous. "The larva has no special characteristics and resembles many other Gastropod veligers, the simple outer lip being hardly incurved indicating a short larval life as probably the velum will not be large". . . . "it seems evident that they stay only for a short time swimming in the plankton, and the shape of the velum probably does not change". Older larvae have not been reared or captured in the plankton, apart from a single large planktonic larva, height of shell 480 μ, with 2 to $2^{1}/_{4}$ whorls, which had already lost its velum and which showed the first indications of the adult sculpture on its last whorl (figured by Lebour l. c. pl. 1 figs. 8—9).

B. Own remarks. Dr. G. Gustafson has observed spawning in this species in the Gullmarfjord (Bohuslän, Swedish W. coast) in aquaria during the first half of August. The balloon-shaped slimy egg masses are attached by a slimy string to the muddy bottom just as the egg masses of *Scoloplos armiger* (see pp. 78—79) and are of nearly the same shape and size. A hundred and fifty adults kept in aquaria in the same locality from $^{25}/_{8}$ to $^{12}/_{9}$-1945 did not spawn at all. Dr. Gustafson is also of opinion that the pelagic stage is suppressed or very short. He has kindly allowed me to mention his observations. — In spite of zealous search, I have been unable to find these larvae in the Sound plankton. Some of them may probably have been inserted in the lists under the designation "small larvae of Prosobranchs sp.", but even if this is the case, they were only met with in very small numbers and play no important part in the plankton. Hence, I am able to confirm the conjecture of Lebour and Gustafson, viz. that the pelagic life is very short. — On August 20th, 1936, however, a single large larva was found (fig. 107), which in size as well as in shape agreed closely with the large *Turritella* larvae figured by Lebour (see above). Also on a comparison of the apices the larva will be referred to *Turritella communis*. As was the case with the large larva from Plymouth, my large larva had also lost the velum. The shell was of a pale horn colour with a reddish-brown columella. This is the only large larva of *Turritella* which was met with during the whole investigation, and no transitional stages between the "small larvae of Prosobranchs sp." and this stage were seen. The large larva was probably a young bottom stage which had metamorphosed in "mid-water" (cf. pp. 466—467). Thus it can be taken for granted that the pelagic stage of this species is very short and of no importance in the plankton.

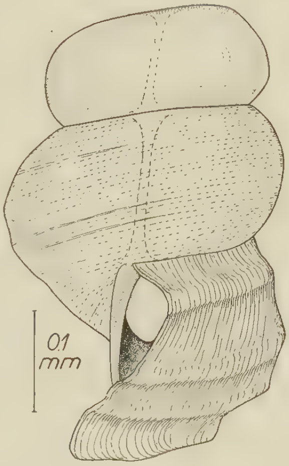


Fig. 107. Young stage found in the plankton, presumably belonging to *Turritella communis* Risso (see the text p. 189). The velum is already lost and the stage found seems to have metamorphosed floating in the water (cf. pp. 466—467). Taken in plankton off Ven, depth 16-0 m, on $^{20}/_{8}$-1936 and drawn from life on the same day.

Coecum glabrum (Montagu). Only larvae are known from the Sound. Living adult specimens are not known from the Danish seas. The nearest locality known for living adult specimens is the area off the island of Bonden, Gullmarfjord (Odhner 1937); empty shells are known from Frederikshavn, N.W. Kattegat.

Reproduction: A. Literature. The reproduction of this species is described and figured by Götze (1938) from Heligoland. Breeding in July-August. The egg capsules, laid in sand, are globular, 150 μ across, with a slightly granulated surface. Each capsule contains only a single egg (about 70 μ in diameter), which develops within the capsule into a rotating embryo. The hatching larvae are typical veligers with a bilobed velum, a shell with one whorl, and a very large operculum. Eyes and statocysts distinct. Larvae in this stage are quite colourless. — Lebour (1936, 1937 a) has described and figured the larvae of the closely related *Coecum imperforatum* from Plymouth plankton and has reared them through metamorphosis. "The shell is a flat spiral and the animal has a yellow digestive gland and is dark purple near the head". The velum is bilobed with a purple border. Older veligers with $2^{1}/_{2}$ whorls have a "spiral-planorbiform shell, body whorl beginning to uncoil and aperture round". They are 320 μ across the shell.

B. Own remarks. Larvae of *Coecum* in all stages of development are rather common in autumn plankton in the Sound. The older stages (fig. 108 E-F) are very similar to those figured by LEBOUR for *Coecum imperforatum*, but as this species is absent from our seas and the adjacent areas, and *C. glabrum* is the only northern species, the larvae should be referred to that species. The youngest larvae of *Coecum glabrum* (fig. 108 A-B) found in the Sound have $1^1/_2$–$1^3/_4$ whorls on the shell (240 μ across), which is spiral-planorbiform like the larvae of *C. imperforatum*. The velum has a purplish-black border of pigment, the operculum is thick.

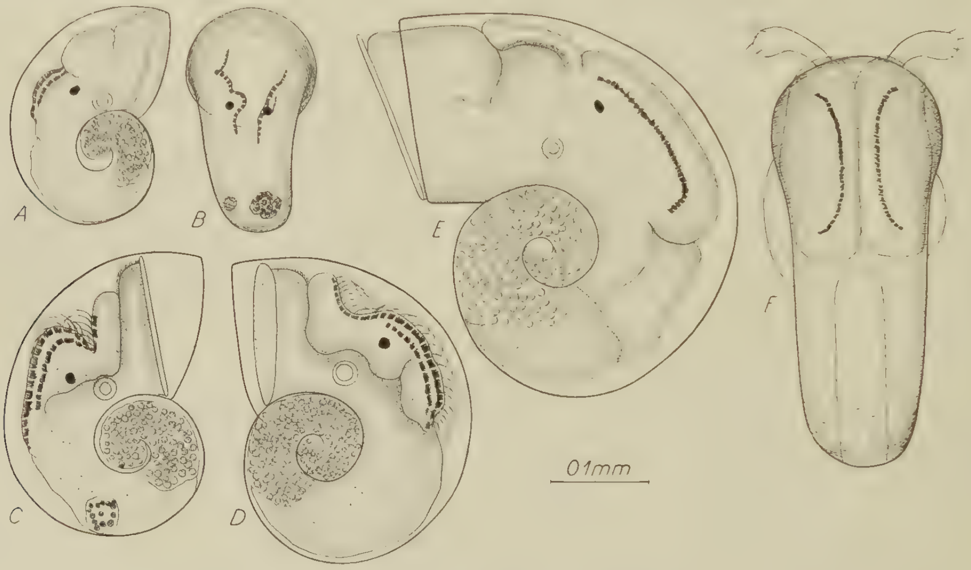


Fig. 108 A-F. *Coecum glabrum* (MONTAGU). Larvae from plankton off Ven, depth 18-0 m, drawn from life. — *A*. Young larva, seen from the right side. — *B*. Larva in a similar stage, seen from the dorsal side (both drawn on $^4/_9$-1937). — *C* and *D*. Medium-sized larvae, seen from the right side (*C*, drawn on $^{17}/_{10}$-1936) and the left side (*D*, drawn on $^4/_9$-1937). — *E* and *F*. Oldest planktonic stage found ("swimming-crawling stage"), seen from the left side (E) and from the dorsal side (F), drawn on $^{18}/_{12}$-1937.

Purplish-black pigment is seen on the wall of the hindmost part of the intestine, and the liver is yellowish-brown. Two large eyes, two large statocysts. When the shell is 380 μ across, the whorl begins to uncoil and to develop into the slightly bent tube characteristic of the adults (fig. 108 E). Larvae in which the largest shell diameter is 410 μ (fig. 108 E-F) are in the swimming-crawling stage with two large club-shaped tentacles. These are the oldest stages known from our plankton.

In the Sound larvae were taken in the plankton off Ven on: $^{17}/_{10}$-36 (6 spms.); $^{14}/_{11}$-36 (1 spm.); $^4/_9$-37 (4 spms. in all stages of development); $^{24}/_9$-37 (1 large spm.); $^9/_{10}$-37 (6 large spms.); $^{23}/_{10}$-37 (7 large spms.); $^{14}/_{11}$-37 (1 large spm.); $^{18}/_{12}$-37 (2 spms., in the swimming-crawling stage); $^6/_1$-38 (1 young spm.); $^{29}/_8$-38 (1 spm.); $^{24}/_9$-38 (2 large spms.), and $^{16}/_9$-39 (8 spms. in all stages), and at Helsingør on: $^{17}/_9$-41 (21 spms.); $^{17}/_{10}$-41 (7 spms., one of them with uncoiled whorl); $^{25}/_{10}$-41 (2 large spms.); $^{11}/_{11}$-41 (1 large spm.), and $^5/_9$-42 (10 spms. in all stages of development). The main season of occurrence is thus from September to November.

The youngest larvae found are so small that they may be supposed to be derived from parents in the nearest neighbourhood of the Sound or the Sound itself. As is well known *Coecum glabrum* together with *Amphioxus*, *Polygordius*, the Tectibranch *Philinoglossa helgolandica*, and the small Nudibranchs *Mikrohedyle glandulifera* and *Hedylopsis suecica* are associated with a certain type of very coarse shelly gravel (Götze 1938, Odhner 1937, Hertling 1930, 1932a) forming a special animal community. Experience seems to show that wherever this type of bottom is found in connection with a favourable salinity, all the above-mentioned species will occur. As very young larvae of *Amphioxus* are also common in autumn plankton in the Sound, there can hardly be any doubt that the biotope as well as the community mentioned above may be found in the Sound also, where it has hitherto been overlooked. The occurrence of these larvae in the autumn suggests, according to our experience, that the adults live in deeper water, i. e. in the Kattegat water.

Bittium reticulatum (Da Costa). Northern and middle parts of the Sound, apparently not very common.

Reproduction: A. Literature. The egg mass, described by Meyer & Möbius (1872, with figure), Lo Bianco (1888), and Lebour (1936), is a slimy coil of a length of about 25 mm rolled up in a spiral or irregularly folded on itself ("doubled twice on itself"), and contains "very opaque eggs, causing the whole to appear white". Breeding near Naples from January to May, near Plymouth in July. Aurivillius (1898b) near Kristineberg found young with shells 2 mm long among *Zostera* from late July and throughout the autumn. Late larvae (very small figures, with few details, only in Lebour, l. c.) have a colourless velum, a pale horn-coloured shell "of $2^{1}/_{2}$ much rounded whorls, and an outer lip, which is produced into a large process". Metamorphosis when the height of the shell is 320 μ.

B. Own remarks. Several specimens were observed spawning in Isefjord on $^{5}/_{6}$-43. The egg masses (fig. 109 A) are narrow gelatinous spirals twined clockwise. The slime is yellowish or colourless, the eggs yellowish-white, and the whole egg mass is attached to *Fucus serratus* or to empty shells of *Mya arenaria*. Three egg masses examined contained 580, 990, and 750 eggs respectively, and the individual egg (fig. 109 B-C) was 60—65 μ in diameter, and surrounded by a cocoon, 95—110 μ across. — Larvae of this species are very common in the Sound plankton, where they occur in all stages of development. They were taken off Ven on: August 1936 (large spms.); $^{13}/_{9}$-36 (1 large spm.); $^{26\text{-}27}/_{9}$-36 (a few older spms.); $^{17}/_{10}$-36 (a few large spms.); $^{1}/_{11}$-36 (1 large spm.); $^{2}/_{8}$-37; $^{12\text{-}13}/_{8}$-37 (several large spms.); $^{21}/_{8}$-37 (7 large spms.); $^{4}/_{9}$-37 (6 spms.); $^{12}/_{9}$-37 (6 spms.); $^{14}/_{11}$-37 (1 large spm.); $^{18}/_{12}$-37 (3 young spms.); $^{5}/_{1}$-38 (1 young spm.); $^{18}/_{6}$-38 (8 young spms.); $^{1}/_{7}$-38 (10 spms.); $^{22}/_{7}$-38; $^{1}/_{8}$-38 (1 large spm.); $^{26}/_{8}$-38 (7 large spms., partially in the swimming crawling stages); $^{11}/_{9}$-38 (1 young spm.); $^{25}/_{9}$-38; $^{8}/_{10}$-38 (2 spms.); $^{17}/_{5}$-39 (7 young spms.); $^{4}/_{6}$-39 (about 70 young spms.); $^{17}/_{6}$-39 (17 spms. in all stages); $^{3}/_{7}$-37 (4 spms.); $^{15}/_{7}$-39 (about 30 spms., most of them young); $^{5}/_{8}$-39 (3 spms.); $^{18}/_{8}$-39 (1 spm.), and off Helsingør on: $^{17}/_{9}$-41 (17 large spms.); $^{7}/_{10}$-41 (6 large spms.); $^{25}/_{10}$-41 (3 large spms.); $^{18}/_{7}$-42 (12 young and old larvae); $^{25}/_{7}$-42 (310 spms., most of them newly hatched); $^{17}/_{8}$-42 (105 spms. in all stages; young larvae dominating), and $^{5}/_{9}$-42 (about 65 spms., most of them older larvae). The main season is thus from late July to early November. The larvae are much commoner than might be assumed judging from the frequency of the adults, but the large number of just hatched larvae (e. g. on $^{25}/_{7}$-42) seems to show that the brood originates from parents living in the Sound itself. In the Limfjord (N. Jutland), where adult specimens are extremely common in the *Zostera*-meadows, the larvae are present in summer plankton in such large quantities that they far outweigh all other larvae of bottom animals there. In such localities we encounter what might be called a "*Bittium*-plankton". The occurrence of the *Bittium*-larvae in the Sound rather late in the summer (in contrast to the larvae of such shallow water forms as for instance *Littorina littorea* and *Mytilus edulis)* seems to show that the adult specimens of *Bittium* have their habitat in somewhat deeper water.

When just hatched, the larva has a brownish, horn-coloured shell, 170 μ across, with much rounded whorls and with a large beak on the outer lip (fig. 109 D). Older larvae (fig. 109 E-G) are of a still darker horn-colour and have very faintly punctured spiral lines on the shell. The columella is reddish-brown, and the outer lip has a marked rectangular process, owing to which the shell is very easy to recognise. The velum, like the whole larva, is quite colourless; the right velar lobe is somewhat larger than the left. The front part of the foot is cylindrical; the liver is yellowish-brown at the top and brownish-black nearest the mouth of the shell. Two black eyes, and two broad tentacles. The larger planktonic specimens found had a height of the shell of 320—330 μ.

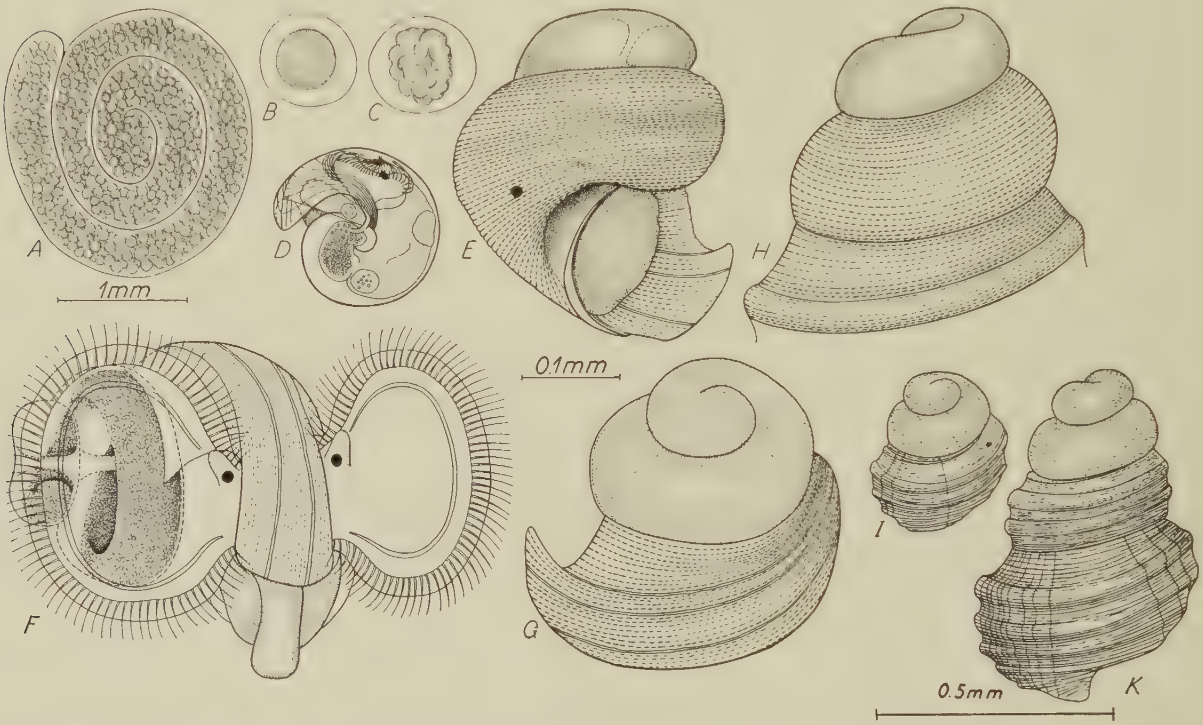


Fig. 109 A-K. *Bittium reticulatum* (DA COSTA). Egg masses and development. *A*. Egg mass of medium size (580 embryos) on *Fucus serratus*; seen from above. Taken in the Isefjord off Nykobing, depth 4-5 m, on $^{5}/_{6}$-1943 (drawn from life on $^{7}/_{6}$-1943). — *B*. Uncleaved egg and *C*. Young embryo from egg-masses (same locality and dates as A). — *D*. Youngest planktonic larva found, seen from the left side. From plankton in Gamborg Fjord (at the Little Belt), depth 2-0 m, caught and drawn from life on $^{20}/_{7}$-1944. — *E* to *G*. Old larvae from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{6}/_{8}$-1936 (fig. E and G) and on $^{8}/_{8}$-1942 (fig. F). Seen from the ventro-lateral side (E) with the black eye showing through the shell; from the front, swimming (F), and from the dorso-lateral side (G). — *H*. Apex of young bottom stage. — *I* and *K*. Young bottom-stages (H to K from Nykobing Mors (the Limfjord), caught and drawn from life on $^{11}/_{7}$-1940).

Triphora perversa (Linné). One living specimen found S.E. of Lous Flak at a depth of 21 m in the summer of 1935 (verbal information from fil. lic. Per-Magnus Lovén, Malmö Museum). This is the only find of adults known from the Sound.

Reproduction: A. Literature. Pelseneer (1926 a) describes the spawn from Roscoff: Gelatinous capsules laid in one layer on empty shells of Lamellibranchs. The hatching larvae are sinistral. The shell has one whorl. Pelseneer (l. c., with figures), P. Fischer (1884), and Lebour (1933 d, with figures; 1937 a) describe the planktonic veliger larvae. Larvae one or two days old, 160 μ across the shell, were sculptured with dots on the whorls; the outer lip is slightly produced and incurved. "The colour of the shell is brown, and it is rather thick and not very transparent". Animal pale, yellowish-white, velum 180 μ across with two almost round, colourless lobes. "When the shell measures 0.64 mm long there are 6—7 whorls, the first one and a half dotted, the next five striated with a slight keel at the periphery, altering at the seventh whorl into the adult, tuberculated sculpture. The last part of the seventh whorl and the eighth are beginning to be tuberculate on each side of the keel". The outer lip is produced into a distinct process. Animal and velum colourless. Larvae with 7—7$^1/_2$ whorls will lose the velum and sink to the bottom. Long larval life (some months?). Breeding-season near Plymouth from late May to the early autumn. Near Kristineberg Aurivillius (1898 b) found bottom stages, 3 mm long, by the middle of October.

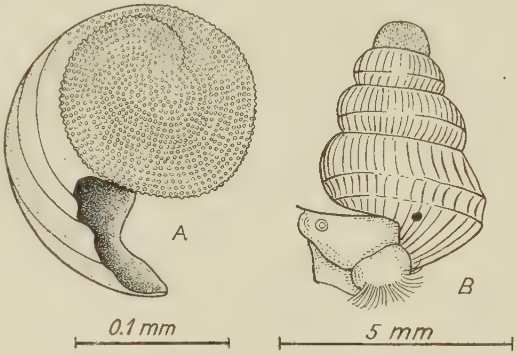


Fig. 110 A-B. *Triphora perversa* (Linné). Larvae from plankton off Ven, depth 18-0 m. — *A*. Young larva with its dotted top-whorl. Caught on $^{24}/_{9}$-1938 (drawn dead the next day). — *B*. Old larva nearly ready to metamorphose. Caught and drawn from life on $^{11}/_{8}$-1936.

B. Own remarks. The larva of *Triphora* is rare in the plankton. In the Sound it was taken off Ven on: $^{11}/_{8}$-36 (1 larva with 5 whorls); $^{11}/_{9}$-38 (1 young larva); $^{24}/_{9}$-38 (1 very young larva), and off Helsingør on: $^{17}/_{9}$-41 (1 young larva), and $^{25}/_{7}$-42 (1 larva with 2 whorls). The main season is thus the late summer and early autumn. The quite young larvae, which had apparently been hatched a few days or hours before, seemed to have originated from parents living in the Sound or its nearest neighbourhood, a fact which seems to show that the adults are somewhat commoner in the Sound than hitherto assumed.

The larvae (fig. 110 A—B) are easily recognisable in the plankton by their sinistral shells, which are of a bright, reddish-purple colour. They agree on all points with the description given by Lebour (l. c.).

Scala clathrus (Linné). A single specimen is known from Hellebæk, but not found in recent years. Empty shells in the northern and middle parts of the Sound as far southwards as Rungsted.

Reproduction: A. Literature. Sykes (1905, p. 73) mentions that off Ireland "one was taken with spawn in July, 1901", but gives neither a description nor a figure of the spawn. Karen Vestergaard (1935) has described the egg mass and the young larvae from Frederikshavn, N.W. Kattegat, taken in July, whence adult females spawned in an aquarium with sand. The spawn, 3 cm long, is a winding string of triangular capsules covered with sand. Each capsule is 2 mm high. The larvae, which hatched nine days later through apertures at the distal end of the capsules, had transparent shells, 150 μ across, with a reddish umbilicus and a slightly bilobed velum. Two days later the larvae showed a right tentacle, an unpigmented velum, and black-purplish pigment on the foot. In June to August Lebour (1937 a) near Plymouth found egg masses of this species attached with slime strings to the parents. The capsules attached to the winding string were irregularly polygonal, and covered with fine mud instead of sand. Thus they are rather different from those found by Vestergaard. Lebour (l. c.) writes: "The eggs, 0.48 mm across, hatched out on June 24, the veligers corresponding with those described by Vestergaard". Ankel (1936 a, 1938) states that the species is a protandric hermaphrodite and has peculiar gigantic spermiozeugmas.

B. Own remarks. If the egg size stated by Lebour, viz. 0.48 mm, is correct and not due to a misprint, the egg mass from Plymouth must be different from that from the Kattegat, where the hatching larvae were only 0.15 mm across, and this is probably the case. The mother animal from Frederikshavn was not taken to Copenhagen, and Dr. Vestergaard only knew that it was a species of *Scala*. As far as I could make out, the species observed by her was *Scalaria communis* (Lam.), but later on it has turned out that *Scala turtonis* (Turton) is much commoner on the sandy areas at Frederikshavn, where I have later found it together with egg masses quite similar to that figured by Vestergaard. Hence it may be supposed that the egg mass from the Kattegat is that of *Scala turtonis* and that from Plymouth that of *Scala clathrus* (= *S. communis*). An egg mass of *S. turtonis* (similar to that in fig. 111 A) taken on $^{23}/_{7}$-36 off Frederikshavn, depth 12 m, sandy bottom, was kept in an aquarium, where the larvae hatched immediately. As my sketches show more details than those of Vestergaard, it seems justifiable to reproduce them here (fig. 111 B—C), especially as an empty shell of *S. turtonis* has been taken in the Sound (kind information by Mr. P.-M. Lovén). Their main features are a very marked reddish-brown thickening of the umbilical and columellar areas, and a large bluish-purple excretory organ resembling that of *Philine*. The shell is 180 μ across. Seven days later these larvae, nourished by small green algae, had a still more reddish-brown umbilicus, the shell having been increased by $^{1}/_{4}$ whorl. The slightly bilobed velum was colourless, bluish-purple pigment was present on the foot, the bluish-purple excretory organ was still distinct, the right tentacle well developed, and the left one had just commenced to appear.—Nothing is known about the reproduction of *S. clathrus* from the Sound or from other Danish waters.

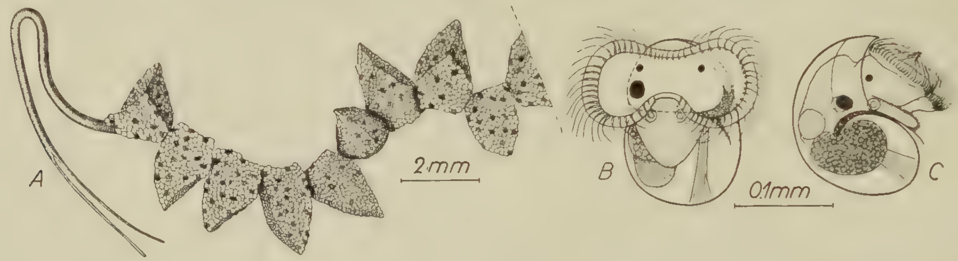


Fig. 111 A-C. *Scala turtonis* (Turton). — *A*. Part of an egg mass. The capsules are situated along the slimy string (the whole egg mass consisted of 160 capsules. Taken off Frederikshavn, July 1936. — *B* and *C*. Planktonic larvae hatched from an egg mass taken off Frederikshavn, depth 12 m, sand bottom, on $^{23}/_{7}$-1936 and drawn from life on the same day. Seen from the ventral side, swimming (B) and from the right side (C).

Aclis minor (Brown) (= **A. supranitida** (S. Wood)). One living specimen found between Gilleleje and Kullen.

Reproduction: A. Literature. Unknown.

B. Own remarks. Larvae of this species, which have been identified on the basis

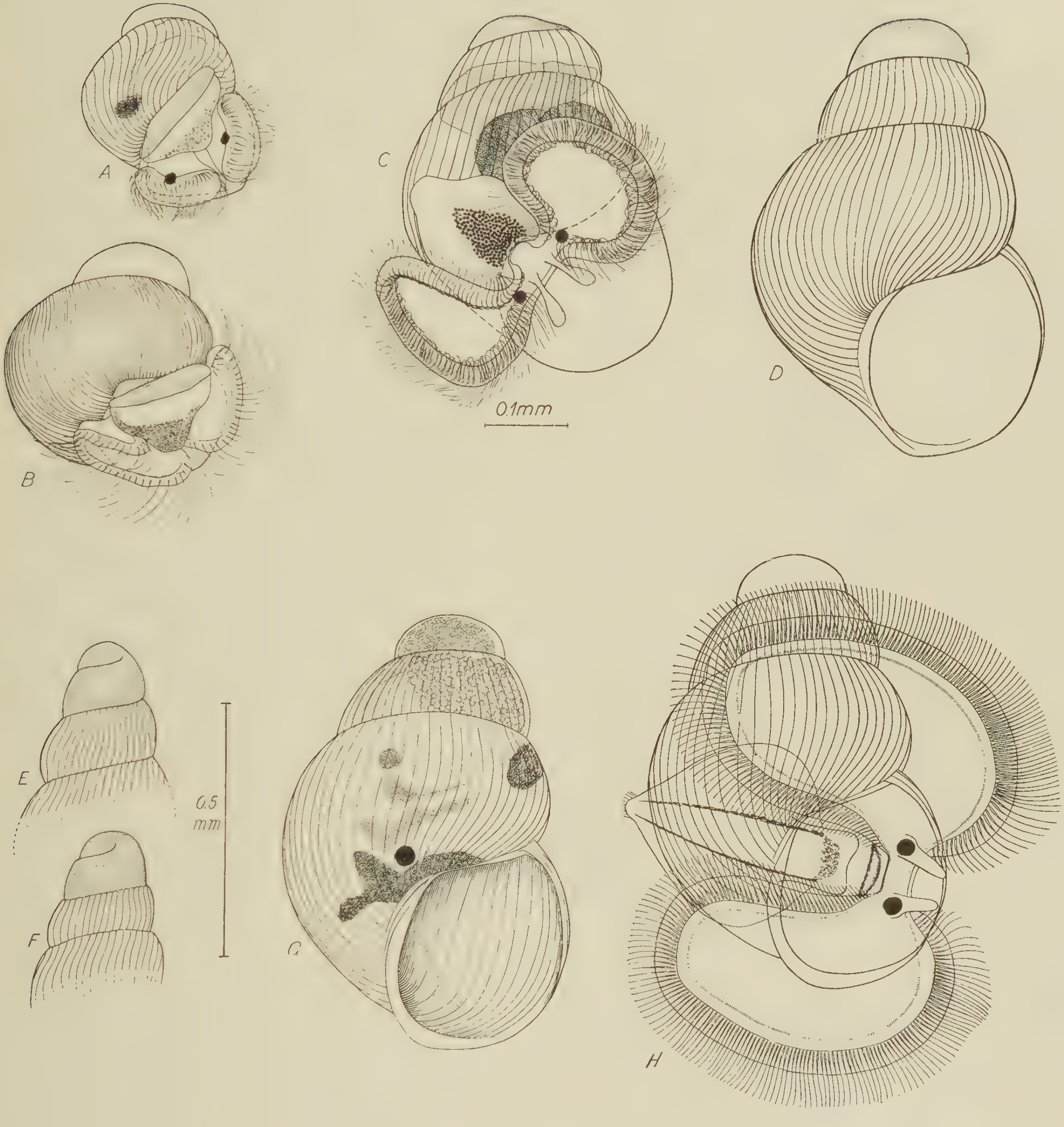


Fig. 112 A-H. *Aclis minor* (Brown). *A* to *D*. Larvae from plankton off Ven, depth 18-0 m, drawn from life on the day of the capture. — *A*. Young larva seen from the ventral side ($^{24}/_{8}$-1936). — *B*. Somewhat older larva seen from the ventral side ($^{24}/_{8}$-1936). — *C*. Old larva with distinct tentacles ($^{29}/_{8}$-1938) — *D*. Shell of oldest planktonic stage known. The larva is in the swimming-crawling stage, the velum is still rather large, the foot long and slender (caught living and drawn on $^{27}/_{9}$-1936). — *E*. Apex of adult *Aclis minor* from the Kattegat. — *F*. Apex of adult *Aclis walleri* taken 33 miles NW. of Højens Fyr, on $^{14}/_{10}$-1904. — *G* and *H*. Old larva from Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40-0 m, caught and drawn from life on $^{22}/_{8}$-1945. Seen withdrawn in its shell (G), and swimming (H).

of a comparison with the apex of the adults, were found off Ven on: $^{20}/_{8}$-36 (1 spm.); $^{24}/_{8}$-36 (4 spms.); $^{26\text{-}27}/_{9}$-36 (about 10 spms. in all stages, the oldest in the crawling stages); $^{28\text{-}29}/_{8}$-38 (one young and one old spm.). The main season is thus August to September, but even in these months the larva is rare; in several years (1937, 1939, 1941 and 1942) it has not been seen at all.

The larvae (fig. 112A -D) are very characteristic and are easily recognisable even among large numbers of other planktonic larvae of Prosobranchs by their faint purplish-blue shell with a purplish-red umbilicus and columella. The youngest larva found (fig. 112A) had two whorls and a height of the shell of 200 μ. The first whorl was quite colourless and structureless, but already the next whorl had a purplish-blue tint and a structure of several regular, but very fine radial furrows. The same structure and colour were found on the third and fourth whorls. The largest larva found (fig. 112 D) had a height of the shell of 550 μ and a large velum, but it was also able to crawl by means of a long slender foot. The propodium may vary in shape very quickly. During their whole development the planktonic larvae have a colourless bilobed velum, the right velar lobe being the larger one, two black eyes, purplish-black pigment around the mouth and along the middle of the foot bordered by reddish-brown dots. The liver is reddish-brown to yellowish-brown, and the stomach has a brownish-black pigmentation. A purplish-black spot is seen through the shell, probably an excretory organ.

Since most of the genera of Prosobranchs occurring in the Sound could be rejected as parents of the larvae dealt with above, only a few possibilities were left; however, owing to the characteristic and rather rare structure found even in the crawling stage with four whorls it was probable that a comparison of the apices might solve the problem, and so it did. Fig. 112 E-F shows the apices of *Aclis minor* and *Aclis walleri*, both with the radial furrows characteristic of our larva, while no apex of this structure was found in any other Prosobranch which might come into consideration. As, furthermore, *A. walleri* is unknown from the inner Danish waters, where *A. minor* is rather common (e. g. in southern Kattegat), the larvae should be referred to the latter species. The purplish-blue tint of the larval shell is not visible on the apex of the adults, but the tint is so faint in the larva, also, that it will disappear when the calcareous layer grows thicker. Also in the Gullmarfjord, where the larvae fig. 112G and H were taken, *Aclis minor* seems to be the only species found within this genus.

Eulima distorta (Deshayes) (= **E. philippi** (Rayn & Ponzi)). Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. Lebour (1935a, 1937a, as *Balcis devians*) describes and figures the larvae from the Plymouth plankton (July to September): "They are much the same size as those of *B.* (*Eulima*) *alba*, but without the black pigment in the animal, the spire of the shell being blunter". "The digestive region in the larva is pale yellowish-brown". "The late larva has four or five whorls with a colourless velum with round lobes. The larva then loses its velum and goes down to the bottom". "The first four or five whorls are quite straight, the curve only beginning apparently after the animal has lost the velum and taken to a life on the bottom". The larval shell is slender and colourless.

B. Own remarks. Larvae were present off Ven on: $^{6}/_{8}$-36 (1 young spm.); $^{17}/_{8}$-36 (1 large spm.); $^{26\text{-}27}/_{9}$-36 (several large spms.); $^{17}/_{10}$-36 (1 spm.); $^{6\text{-}9}/_{8}$-37 (2 spms., one of them with 5 whorls); $^{23}/_{10}$-37 (1 young spm.); $^{11}/_{9}$-38 (1 spm. of medium size), and off Helsingør on: $^{17}/_{8}$-42 (1 young spm.). The main season is thus from August to October, but the larva is rather rare in the plankton.

The larva with $2^1/_2$ whorls, 300 μ high (fig. 113 A), agrees well with the description of Lebour (l. c.) in being colourless, apart from a very pale purplish pigmentation on the foot. Already in this stage two large tentacles have developed, and the shell has a very typical suture like a hoop tightly attached to the preceding whorl — a feature very characteristic of the *Eulima*-shells. Two large velar lobes, two large black eyes, yellowish-green liver, and stomach with a purplish tint. Shell quite smooth, shining. The older larvae (5 whorls, cf. fig. 113 B-C), however, have a very characteristic purplish-blue pigmentation on the trilobed foot. The stomach is also purplish-blue, and the liver is yellowish-brown. There is, however, no black pigment round the mouth and in the oesophagus, as found in the closely related larva of *Eulima alba* (Lebour 1935 a, p. 67). The bilobed velum is still colourless. In this stage the shell has a height of 540 μ and a maximum breadth of 300 μ; stages later than this have not been seen in the plankton. The fact that just hatched larvae were found in our samples near Ven seems to indicate that they originate from parents living in the Sound. As, however, *Eulima distorta* is the only species of *Eulima* living there, the identity seems to be rather certain.

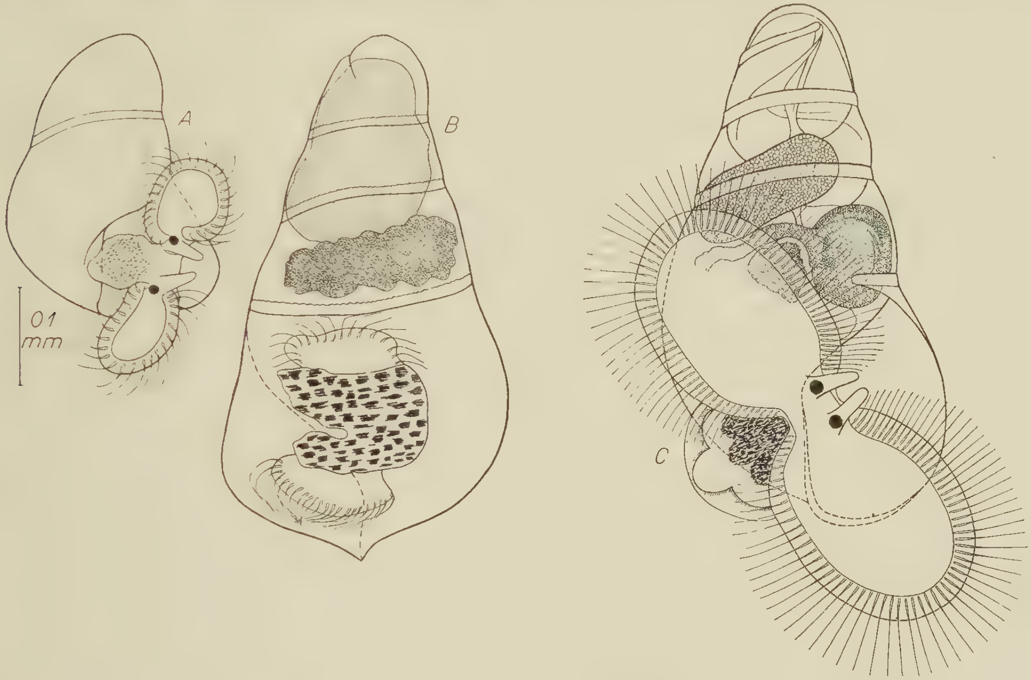


Fig. 113 A-C. *Eulima distorta* (Deshayes). *A* and *B*. Larvae from plankton off Ven, depth 15-0 m, drawn from life on the day of the capture. — *A*. Young larva with the velum extended ($^6/_8$-1936). — *B*. Larva near the stage of metamorphosis, with the animal withdrawn in its shell ($^{17}/_8$-1936). — *C*. Old larva, swimming, seen from the ventral side. From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40-0 m, caught and drawn from life on $^{17}/_8$-1945. The adults are extremely common in this latter locality.

Eulima intermedia Cantraine. Living specimens known from Kullen-Hellebæk, rare. Reproduction: Unknown in the literature. No observations from the Sound.

Pelseneeria stylifera (Turton). A single specimen known from Skovshoved, attached to *Strongylocentrotus droebachiensis*; not found in the Sound for the last 60 years.

Reproduction: A. Literature. Jeffreys (1867) describes the egg masses, which are likewise described and figured by Lebour (1932, 1937 a) and Ankel (1938). The adults live as parasites on the outer dorsal surface of *Strongylocentrotus* or *Psammechinus*, and the eggs are laid here in cocoons, 1.2 × 1.1 mm, which are attached singly to the surface of the Echinid by short stalks; several egg cocoons may be found on one Echinid. Each egg sac contains from 60 to 400 eggs, 100 μ across, which all develop into larvae. At the same time the egg cocoon swells to more than double its size. Both egg sacs and eggs are colourless and transparent. The newly hatched larva, 130 μ across the pale horn-coloured shell, which has one whorl, is nearly round. Velum colourless, foot short and round, eyes far apart. Larvae two days old have developed the right tentacle. Statocysts distinct. Older larvae not described; the young larvae may easily be confused with other young larvae of Prosobranchs.

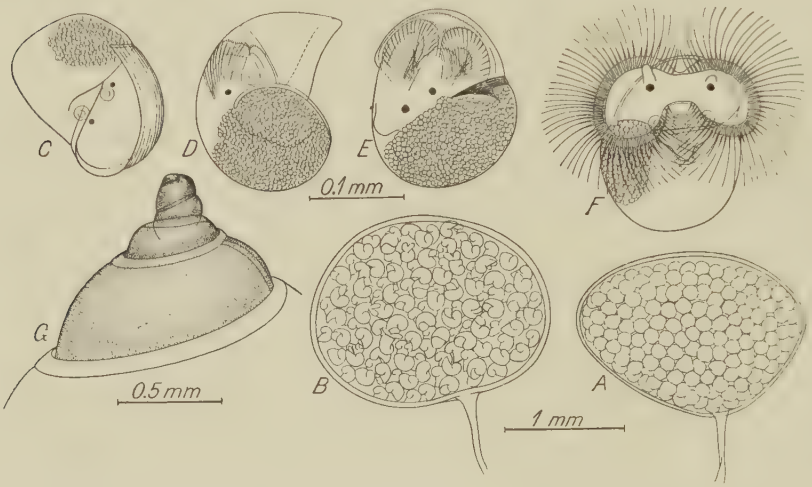


Fig. 114 A-G. *Pelseneeria stylifera* (Turton). *A* and *B*. Egg cocoons with uncleaved eggs (A) and with embryos in the hatching stage (B). Taken off Flatholmen (Bohuslän, Swedish W. coast), depth 40 m, on $^{17}/_{8}$-1945, situated between the spines of *Psammechinus miliaris* (drawn from life the same day). —*C* to *F*. Larvae just hatched seen from the ventral side (C), directly from the apex (D), from the dorsal side (E), and from the ventral side, swimming (F). Drawn from life on $^{21}/_{8}$-1945.—*D*. Apex of adult specimen from the same locality.

B. Own remarks. Nothing is known from the Sound about the reproduction. —During a stay at the Swedish zoological station, Kristineberg (Bohuslän, Swedish W. coast), a specimen of *Psammechinus miliaris* taken off Flatholmen, depth 40 m, on $^{17}/_{8}$-1945, with two adults and 25 egg cocoons of *Pelseneeria* was placed at my disposal. The balloon-shaped, colourless cocoons (fig. 114 A-B) were fastened by their short stalks around the bases of the spines of *Psammechinus*. When I tried to remove a cocoon by the aid of a needle, a pincet or a scalpel, all spines in the vicinity were actively directed towards the instrument, and in this way the egg cocoons are exceedingly well protected. —Some of the cocoons contained uncleaved, yellow eggs about 115 μ across (eggs from Plymouth 100 μ across) (fig. 114 A), others contained whitish veligers with colourless shells and others again old veligers with horn-coloured shells.

Some of the old embryos (fig. 114 C-F) hatched in a natural way on $^{21}/_{8}$ with a horn-coloured shell 170—190 μ across (shells from Plymouth 130 μ across), 175 to 180 μ high and with $1^{1}/_{4}$ whorls. The columella is of a dark horny colour and the animal is only with difficulty seen through the rather opaque shell. The granulated liver is yellowish-brown. Two black eyes, two distinct statocysts. The swimming veliger (fig. 114 F) has a colourless, bilobed velum with long coarse cilia. The right velar lobe and the right tentacle are much bigger than the left ones. The small foot has a faint purplish pigmentation in the middle.

The apex of the adult animal (fig. 114 G) is provided with $2^{1}/_{2}$—3 embryonic whorls of the same horn colour as found in the shells of young larvae. The shape of the adult whorls is totally different from that of the larval ones, and it must be taken for granted that the species has a rather long pelagic life. A careful search for such larvae in Kristineberg plankton in August—September 1945, however, gave a negative result.

General Remarks on Pyramidellid Larvae.

The apices of adult *Pyramidellidae* present two quite different types, viz. apices on which a scalariform, sinistral larval shell is placed nearly quite freely horizontally across the top of the regular whorls of the adult dextral shell (e. g. in *Odostomia conoidea, O. acuta, O. unidentata, O. turrita, O. plicata, O. albella, Turbonilla rufa, T. lactea, Eulimella scillae, E. acicula*, and *E. nitidissima*, cf. pp. 210—210, figs. 115 A-G, 116—119, 121—123), and apices in which no sinistral larval shell is seen at the top and all the whorls visible have a normal dextral appearance (e. g. in *Brachystomia rissoides, B. eulimoides, Parthenina decussata, P. indistincta, P. interstincta, Evalea insculpta, E. obliqua, Liostomia clavula* and *Partidula spiralis*, cf. pp. 201 and 206, figs. 115 H-Q, 120).

We know that larvae with scalariform, sinistral shells like those found on the apices of the first group are common in the plankton (cf. Lebour, 1936, pl. II, figs. 18, 19 and 20), and it can be taken for granted that forms with this type of apex have a pelagic larval stage. Concerning the group of species in which no sinistral larval shell is seen at the top, we know, however, that *Brachystomia rissoides* has a non-pelagic larval development near France (Ankel 1936a, p. 165 and p. 215, Pelseneer 1914), probably an extremely short larval life in Vellerup Vig (the Isefjord, Denmark, Rasmussen 1944) and in the Sound (cf. this paper pp. 204—205), and a non-pelagic development at Frederikssund (Roskilde Fjord, unpublished). As to another species within this group, viz. *Odostomia eulimoides*, Lebour (1932) states that "it probably only lives a short time as a veliger and is not important as a planktonic larva". The shells figured by her are sinistral but without any scalariform tendency. Also the third species within this group, the larva of which has been seen, viz. *Parthenina decussata*, seems to have a very short pelagic life (Lebour 1936, p. 556, pl. II, figs. 13—14). When the apex of such forms with no outer larval shell at the top is broken up and examined internally, not the slightest trace of a larval shell can be found. I have tried such preparations on several different species.

Thus it can be stated that species within the *Pyramidellidae* which have a scalariform, sinistral larval shell lying horizontally across the top of the apex reproduce by pelagic, scalariform, sinistral larvae easily recognisable in the plankton, and that species in which no such larval shell is visible at the top of the apex have either a non-pelagic development or a very short pelagic larval life — or an entirely different type of larval shells.

Lebour (1937 a, p. 141), however, states for all *Pyramidellidae* that ". . . the planktonic young in their early stages having a sinistral shell and a dextral animal, the shell later also being dextral", and that "the early young are thus easy to recognize, at any rate in British waters, where the only truly sinistral planktonic larva is that of *Triphora perversa*". In other words, all sinistral planktonic Gastropod larvae in the northern plankton, apart from those of *Triphora* (and, of course, those of *Limacina*), may be referred to the *Pyramidellidae*.

On starting the investigation in the Sound, I was of the same opinion, but two years later we knew a large series of sinistral-shelled larvae with dextral animals which had flat helicoid shells (cf. fig. 144—157) rather different from the scalariform type hitherto recorded from *Pyramidellidae*. If all these helicoid larvae really belonged to the group of *Pyramidellidae* without visible larval shells on the apex, it was a dilemma to find a sufficient number of parent species in the Sound and the adjacent waters to cover all the species of larvae found!

Finally, after several years of search it turned out that all the sinistral helicoid larvae with dextral animals belonged to the *Tectibranchiata* and the *Ascoglossa* (*Cylichna, Retusa, Utriculus, Acera, Philine, Limapontia, Stiliger* etc., cf. pp. 245–268, figs. 144–157), which were gradually reared through metamorphosis. Thus the larvae figured by Lebour 1936, pl. II, fig. 21 and referred by her to the *Pyramidellidae* are actually typical larvae of Tectibranchs, probably belonging to *Diaphana hyalina* (cf. p. 251, fig. 147 A—B).

The facts given above show that adult *Pyramidellidae* with no visible larval shell on top of the apex have a much reduced pelagic life or no pelagic stage at all. When a planktonic stage is present in such forms, this will probably be so short that the larvae will play quite a minimal part in the plankton. In the Sound we have never seen such larvae, which, however, may very easily have been overlooked. The scalariform, sinistral larvae belonging to the other group of *Pyramidellidae* will be dealt with below under the individual species.

The systematic position of the *Pyramidellidae* is still very dubious, and their placing within the Stirps *Aglossa* must be regarded as a provisional and artificial arrangement. Detailed anatomical studies — as far as I know — are not available, and the radula otherwise used to trace the systematic position in Gastropods is absent in this family. No doubt a detailed anatomical investigation of the *Pyramidellidae* will provide new aspects as to their systematical position. — The biological dates on *Pyramidellidae* now available show also clearly that a systematical revision is highly desired. In contrast to the surrounding groups of Prosobranchs the *Pyramidellidae* are hermaphrodites (cf. a. o. Pelseneer 1899 a). While the surrounding groups of Prosobranchs deposit their eggs in capsules, the *Pyramidellidae* spawn egg masses of the mucus-like type so well known among Opisthobranchs, and — as in Opisthobranchs, but in contrast to all Prosobranchs — the *Pyramidellid*-eggs are connected by a "calaza" from capsule to capsule like pearls on a string. Finally: the sinistral-shelled veligers with their large coloured excretory organs so characteristic of the *Pyramidellidae* are quite isolated within the Prosobranchs but show a striking resemblance to the sinistral veligers, which according to this paper seem to constitute the normal larval type in Tectibranchs and Ascoglossids, and in both cases the sinistral larval shell continues in a dextral adult shell. — These facts combined e. g. with the striking resemblance between the shells of the Tectibranch *Toledonia* (*Ptisanula*) and those of different species of *Odostomia*, as pointed out by Odhner (1914 b, p. 14), and with the common features which connect the shells of e. g. *Odostomia* (*Amaura*) *candida* Møller and shells of the genus *Actaeon*, seem to point to a closer connection between the *Pyramidellidae* and the *Opisthobranchia* than hitherto assumed. Mørch (1865) and Koken (1889) are both of opinion that the Pyramidellids and the Tectibranchs are closely related, while other authors, e. g. Collin (1880) and Petersen (1888), seem to follow Mørch. Pelseneer (1899 a), who studied *Odostomia plicata, Brachystomia rissoides,* and *Partidula spiralis,* is of opinion that the Pyramidellids apart from their hermaphroditism show features (e. g. coalescent cerebral ganglia and pedal ganglia and the "collier aesophagien" situated caudally to the salivary glands) so different from those of the Tectibranchs that he disclaims the relations between these two groups assumed by Mørch and Koken (l. c.). Pelseneer, however, admits that he has had no chance to study the egg masses and larvae of the Pyramidellids.

Our recent knowledge of eggs and larvae of Pyramidellids and Tectibranchs seems, however, to support the assumption of the relations between these two groups to such an extent that the coalescent ganglia mentioned by Pelseneer (l. c.) seem of little value as a counter-

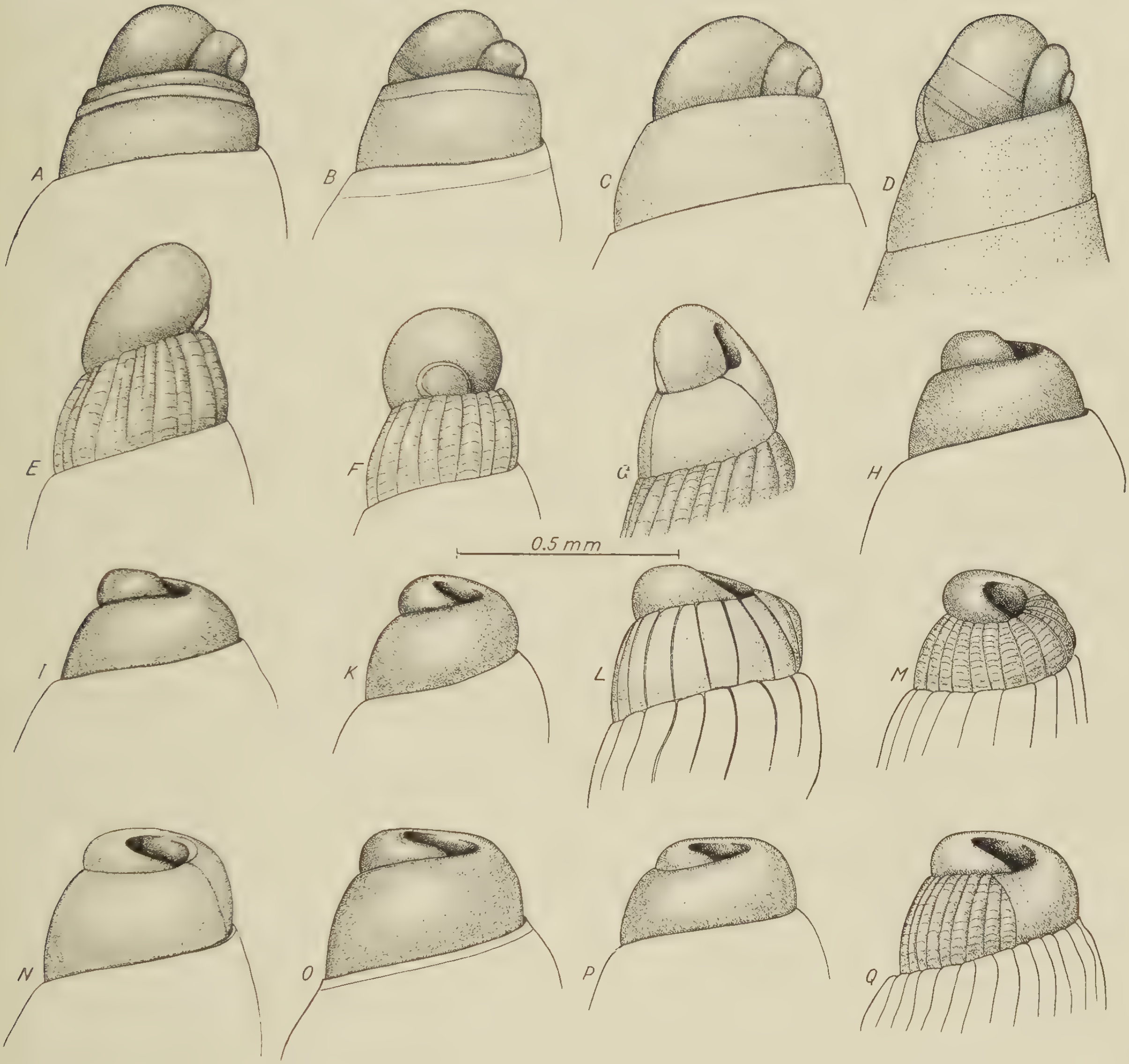


Fig. 115 A-Q. Top-whorls (Apices) of Danish species of *Pyramidellidae* (cf. further figs. 116-124), drawn from specimens kept in the Copenhagen Museum. — *A. Odostomia unidentata* Montagu (51 miles NW.$^1/_4$W. of Hanstholm, depth 254 m, "Thor" St. 1567). — *B. Odostomia plicata* Montagu (Alsted in the Limfjord, ? subfossil). — *C. Odostomia albella* Lovén (Kattegat, "Hauch" St. 474). — *D. Eulimella scillae* (drawn from a British specimen). — *E* and *F* and *G. Turbonilla lactea* (Linné) (locality unknown), seen from the dorsal side of the larval shell (E), the top of the larval shell (F), and the ventral side of the larval shell (G). — *H. Brachystomia rissoides* (Hanley) (Kattegat, "Hauch" St. 370). — *I. Brachystomia eulimoides* Hanley (Sallingsund, the Limfjord). — *K. Parthenina decussata* (Montagu) ("Hauch" St. 500). — *L. Parthenina indistincta* (Montagu) (drawn from a British specimen). — *M. Parthenina interstincta* (Montagu) (Volstrup in the Limfjord, ? subfossil). — *N. Evalea insculpta* (Montagu) (Kattegat, "Hauch" St. 203). — *O. Evalea obliqua* (Alder) (Hellebæk). — *P. Liostomia clavula* (Lovén) (Kattegat, "Hauch", St. 370). — *Q. Partidula spiralis* (Montagu) (2 miles N.$^1/_2$W. of Bulbjerg Baake).

argument, all the more so since the systematic value of the ganglia must be regarded as dubious. The confluent ganglia in Pyramidellids may just as well be connected with the rather sessile life of most of these species (commensals, parasites; compare for instance the conditions in Lamellibranchs with their rather small locomotion).

It is the hope of the present author to clear up these problems during the coming years in collaboration with Dr. H. LEMCHE.

Odostomia conoidea (BROCCHI). A single empty shell known from Hellebæk.

Reproduction: A. Literature. Unknown.

B. Own remarks. The apex bears a sinistral scalariform larval shell (fig. 116 C), and the larva must accordingly be pelagic and seems to have a smaller larval shell than all the other species found in the Danish waters with the larval shell visible on top of the apex. Further, the larval shell, according to the apex of the adults, has a distinct, fairly elevated upper whorl and a rather tumid last whorl. At Helsingør two larvae were taken on $^{25}/_{10}$-41, which had all the characteristics of the larval shell on the apex of *O. conoidea*. The larvae in question (fig. 116 A—B) had a height of the shell of 280 μ (the larval shell on the apex had a height of 280 μ also), and the largest breadth of the shell was 245 μ. The olive-green-brownish liver, two sealing-wax red spots together forming the excretory organ, two large black eyes, and two broad purplish-carmine borders of velar pigment were seen through the transparent shell. Also the otocysts were distinct. — A larva quite similar to that figured here was observed in plankton near Frederikshavn (N.W. Kattegat) on $^{2}/_{8}$-39 (the adult *O. conoidea* seems to be frequent in the adjacent parts of the Skagerak).

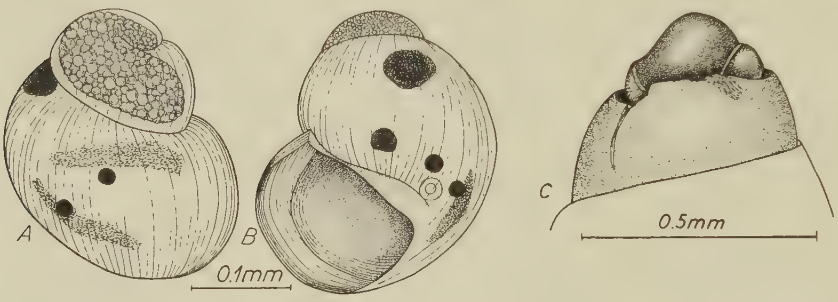


Fig. 116 A-B. Larvae presumably belonging to *Odostomia conoidea* (BROCCHI) (see the text p. 202). From plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{25}/_{10}$ 1941 (drawn from life on $^{26}/_{10}$). Seen from the dorsal side (A), and the ventral side (B) with the animal withdrawn. — *C*. Apex of adult specimen from Skagerak, depth 475 m (from a specimen in the Copenhagen Museum, "Thor" St. 213).

Odostomia acuta JEFFREYS. Northern part of the Sound, rather common locally on clayey bottom at fairly great depths.

Reproduction: A. Literature. Unknown.

B. Own remarks. The larval shell on top of the apex of the adult shell (fig. 117 E) suggests a pelagic larval stage, and further that the larvae are larger and more tumid than those of *Odostomia turrita* (fig. 118 E) and larger, but much less tumid, than those of *Eulimella acicula* (fig. 122 C—D). Larvae which show corresponding characteristics to these and differing from the characteristics of all other Pyramidellids from the Sound were present in the plankton taken off Ven on: $^{6}/_{12}$-36 (1 spm.), and off Helsingør on: $^{19}/_{12}$-41 (1 spm.). The larva is thus only known from December.

The larva (fig. 117 A—B) has two to two and a half whorls. The height of the shell is 320 μ, the largest breadth 270 μ, that is to say it is the largest *Odostomia* larva known from the Sound. The whorls, shining enamel-white in direct light, are transparent and rather tumid. The greenish-brown liver is seen through the shell and so is the sealing-wax red excretory organ, the two black eyes, and the statocysts. The foot has a characteristic bluish-black pigmentation. The velum is quite colourless. — From $^{19}/_{12}$-41 a metamorphosing larva is at hand (fig. 117 C—D), which closely resembles the larva taken on $^{6}/_{12}$-36 in the size and shape of the rather tumid shell and in the bluish-black pigmentation of the foot. The velum is now reduced, the shell has become dextral with a new coarse columella, and the sinistral larval shell has been strengthened with a broader suture. The liver is olive-green, the excretory organ brownish and the two black eyes still distinct. As far as I am aware, this and fig. 119 are the only sketches hitherto published which show exactly the stages of metamorphosis of the *Pyramidellidae.*

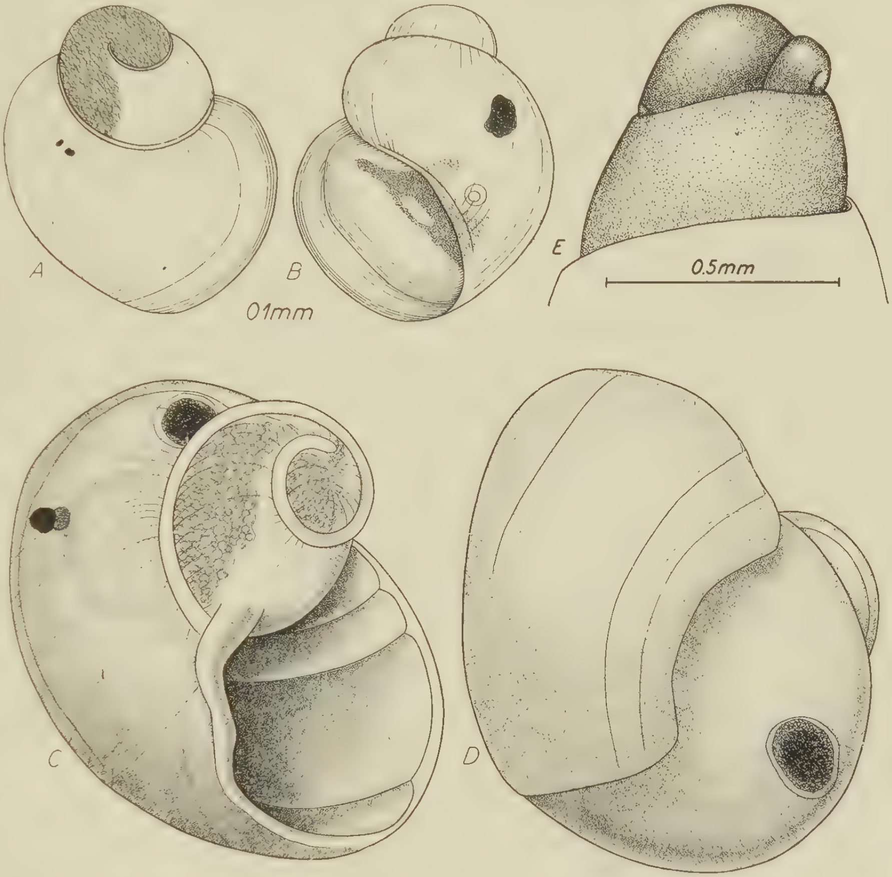


Fig. 117 A-E. *Odostomia acuta* Jeffreys. *A* and *B*. Old larvae from plankton off Ven, depth 18-0 m, on $^{6}/_{12}$-1936 (drawn from life on $^{7}/_{12}$). Seen from the dorsal side (A), and the ventral side (B). — *C* and *D*. Young stage just after metamorphosis. Taken floating in the plankton (cf. "mid-water metamorphosis", pp. 466–467) between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{19}/_{12}$-1941 (drawn from life on $^{20}/_{12}$). Seen from the mouth of the adult shell (C) and from the dorsal side of the adult shell (D) (see the text pp. 202–203). — *E*. Apex of adult specimen from Hellebæk.

Odostomia turrita (Hanley). Common on clayey bottom in the northern and middle parts of the Sound.

Reproduction: A. Literature. Unknown.

B. Own remarks. Apex with a sinistral scalariform larval shell at the top (fig. 118 E). Larval stage accordingly pelagic, with a rather small slender shell. Larvae agreeing with these characteristics were taken off Ven on: $^{17-21}/_{8}$-36 (several large spms.); $^{12-13}/_{9}$-36 (1 spm.); $^{26-27}/_{9}$-36 (several large spms.); $^{17}/_{10}$-36 (1 spm.); $^{19}/_{10}$-36 (1 spm.); $^{14}/_{11}$-36 (1 large spm.); $^{23}/_{7}$-37 (1 spm.); $^{9}/_{8}$-37 (3 spms.); $^{12}/_{8}$-37; $^{21}/_{8}$-37 (3 spms.); $^{4}/_{9}$-37 (1 spm.); $^{9}/_{10}$-37 (1 young spm.); $^{13}/_{8}$-38 (2 spms., one of them quite young); $^{11}/_{9}$-38 (1 young spm.), and $^{24}/_{9}$-38 (2 spms.), and off Helsingør on: $^{5}/_{9}$-42 (2 older and 1 young spm.). Their season of occurrence is thus very sharply delimited and rather short, viz. August to October. The large percentage of quite young larvae shows that they originate, at any rate partially, from parents living in the Sound itself or the adjacent waters.

The oldest larvae found (fig. 118 C-D, 119 A) have a height of the shell of 270—320 μ and a maximum breadth of 200—260 μ (the larval shell on the apex fig. 118 E has a height of 315 μ). The shell is slender, shining, quite colourless, and transparent, the liver is of a dark green colour. Two dark-reddish-purple pigmentations (probably together forming the excretory organ) are visible through the last whorl. The larva has two black eyes, distinct statocysts, and a quite colourless bilobed velum.

This larva is among the commonest Pyramidellid larvae in the Sound. Only the larva of *Eulimella nitidissima* shows a similar frequency.

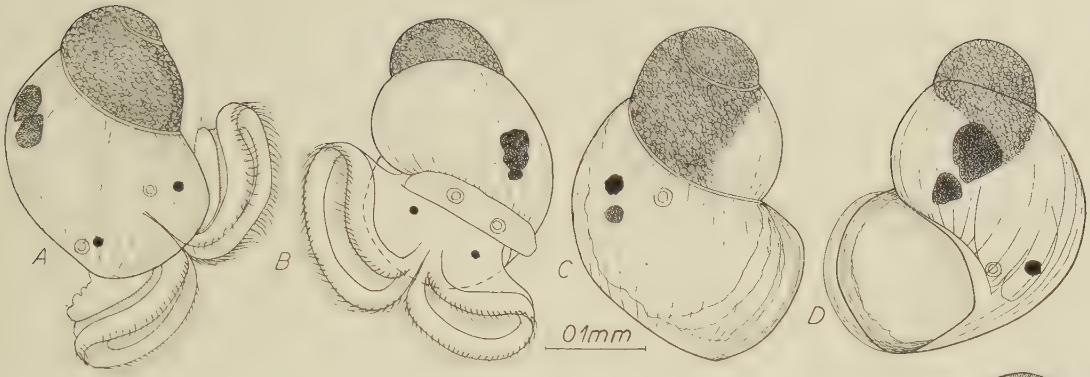
During my stay at the zoological station Kristineberg (Bohuslän, Swedish W. coast) in August 1945 larvae of *Odostomia turrita* were common in the plankton, a fact which is in good agreement with the frequency of the adults in the area. I therefore took the chance to sketch a series of larvae in different phases of metamorphosis (fig. 119 A-G). Fig. 119 A is an old planktonic stage very similar to that sketched from the Sound in fig. 118 C. — Fig. 119 B shows a larva in the same position as fig. 119 A, but now with the first beginning of the dextral shell. The outer lip of the larval shell has commenced to form a columella, and the columella of the larval shell has continued to grow as a new outer lip. Fig. 119 C-D give the same larva in other views. Already here the transverse position of the larval shell at the top of the adult whorls is distinctly indicated. Fig. 119 E, F and G show a somewhat older larva with the first adult whorl fully formed. This series illustrates better than many words the intricate problems of the change from a sinistral to a dextral shell in *Pyramidellidae*. — All the stages figured were found floating in the water masses although the velum was totally reduced. As such metamorphosing larvae occurred rather frequently in the plankton, mid-water metamorphosis (cf. pp. 466—467) does not seem to be uncommon in this species.

Liostomia clavula (Lovén). One specimen (living?) known from Hellebæk. Common in southern Kattegat.

Reproduction: Unknown in the literature as well as from the Sound. Judging from the type of the apex (fig. 115 P) the species has a non-pelagic development or a much shortened planktonic life.

Brachystomia rissoides (Hanley). Northern and middle parts of the Sound, common in *Mytilus* epifauna.

Reproduction: A. Literature. Pelseneer (1899a) has shown that this species is hermaphroditic, and has (1914) described and figured the egg masses and embryos from France: The animal is hermaphroditic. The eggs are deposited on the shells of *Mytilus*, and the individual egg mass forms a thin slimy layer (3 × 2 mm) containing about 50 eggs, each connected with its two neighbours by a string issuing from the egg membrane. The eggs are oval, 380 μ in longest diameter. The larval development takes about 25 days, and the young, 400 μ across the shell, hatch in the crawling stage without any planktonic life. Meyer & Möbius (1872, Suppl., p. 66) mention and figure the eggs from the Bay of Kiel. The eggs are deposited in small heaps, 4 mm in diameter and 2 mm high, in August. According to the figure the egg mass seems to contain about a hundred eggs. Erik Rasmussen (1944, pp. 208—215) describes and figures the egg masses and embryonic development of this species from Vellerup Vig (the Isefjord, Denmark). His results differ in several



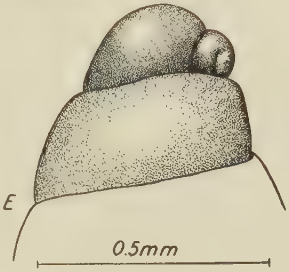


Fig. 118 A-E. *Odostomia turrita* (Hanley). *A* to *D*. Larvae from plankton off Ven, depth 18-0 m, on $^{18}/_{8}$-1936 (drawn from life on $^{19}/_{8}$). — *A* to *B*. Larva of medium size, swimming, seen from the dorsal side (A) and the ventral side (B). — *C* to *D*. Old larva with the animal withdrawn, seen from the dorsal side (C) and the ventral side (D). -*E*. Apex of an adult animal from Hellebæk.

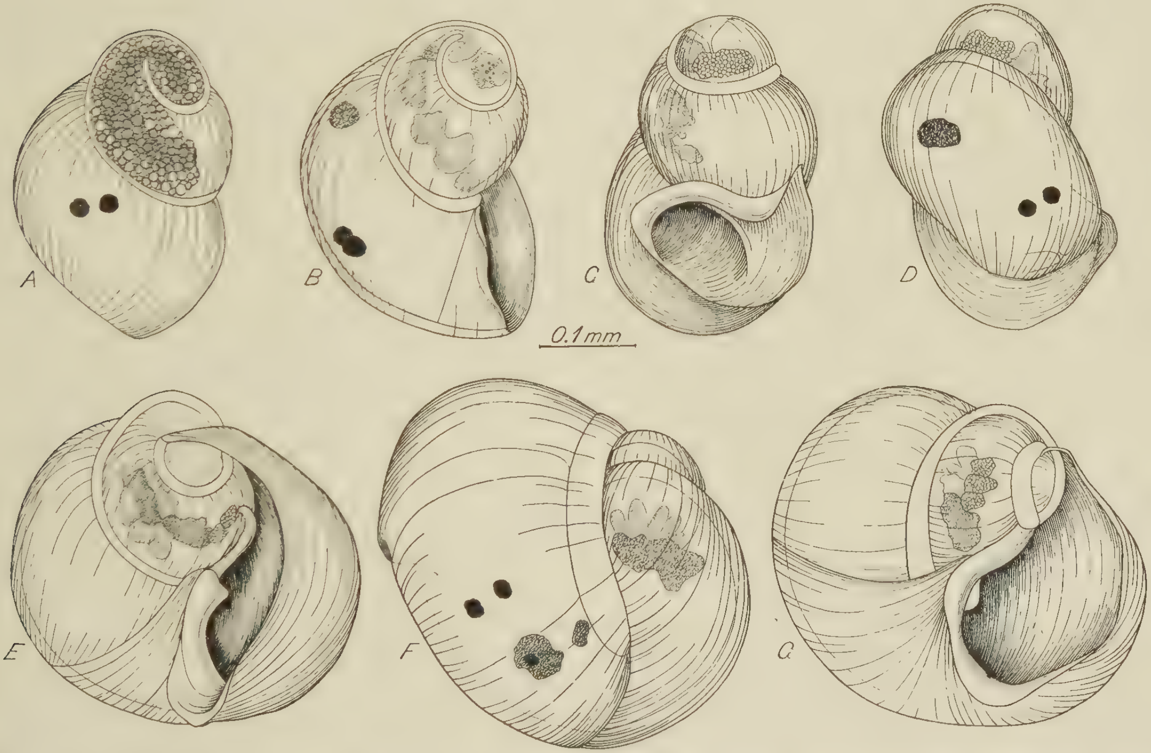


Fig. 119 A-G. *Odostomia turrita* (Hanley). Metamorphosing larvae from plankton off Kristineberg (Bohuslän, Swedish W.coast), depth 30-0 m. Drawn from life on the day of capture. *A*. Old veliger larva, seen from the right side (caught on $^{19}/_{8}$-1945). — *B* to *D*. Larva in the first stage of metamorphosis, seen from the right side (B), the ventral side (C), and the dorsal side (D) of the larval shell (caught on $^{20}/_{8}$-1945). — *E* to *G*. Larva at the end of metamorphosis, seen in different views (caught on $^{19}/_{8}$-1945).

respects from those of Pelseneer. Rasmussen's observations may be summed up as follows: Breeding season May to July. Four adult specimens produced 17 egg masses in eight days. The individual egg mass, about 4.5 mm across (spawned in an aquarium), contains about 500 eggs, 180–200 μ in diameter. At a temperature of 19° C. the development takes about six and a half days, and the larvae, 300 μ across the shell, hatch as colourless veligers with a bilobed, rather small velum, a helicoid sinistral shell, two black eyes, a black excretory organ, and two large statocysts. The length of the free-swimming stage is unknown, but the small velum seems to indicate that the pelagic life is very short. – This is the first example known of a Prosobranch not reproducing by nurse eggs which is able to vary its size of egg and its larval development (pelagic – non-pelagic) from place to place. In the summer of 1944 Erik Rasmussen studied the reproduction of this species near Frederikssund, Roskilde Fjord. Here the eggs were still larger than in the French specimens and the development was quite non-pelagic, thus differing totally from the conditions found at Vellerup Vig. The shape of the shells, the appearance of the animals, and *Mytilus* as the only host seem to be features common to both the French and the Danish populations, and their systematic identity can hardly be questioned.

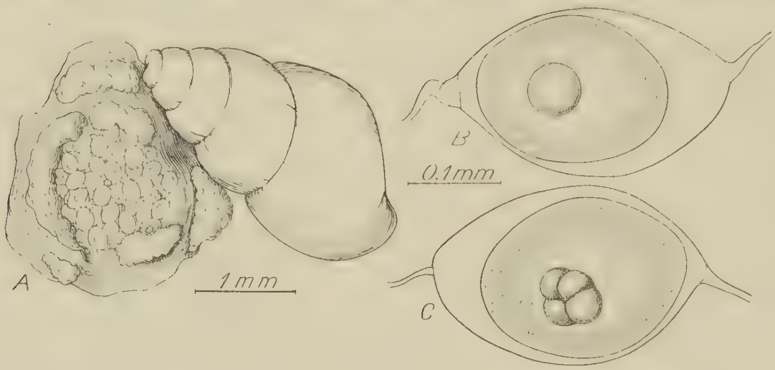


Fig. 120 A-C. *Brachystomia rissoides* (Hanley). *A.* Mother animal in situ on a *Mytilus*-shell with its new-spawned egg mass. Hittarps reef, depth 4 to 8 m, on $^{18}/_{7}$-1945. – *B.* Uncleaved egg from the egg mass fig. 120 A in its egg cocoon. – *C.* Egg cocoon with an egg in the four-cell stage (all figs. drawn from life on $^{18}/_{7}$-1945).

B. Own remarks. An apex of the adult shell is seen in fig. 115 H. — On $^{18}/_{7}$-1945 a few adult specimens af *B. rissoides* were taken on the Hittarp reef, depth 4—8 m, in the normal position on shells of living *Mytilus*. In the laboratory, a few hours later, an adult *Brachystomia* with its newly spawned egg mass was found near the margin of a *Mytilus* shell (fig. 120 A). The egg mass, when discovered, contained only uncleaved eggs, which four hours later were in the four- or eight-cell stages. — The egg mass, 2 to $2^{1}/_{2}$ mm in diameter and about 2 mm high, consisted of a very tough yellowish-colourless slime covering about 230 colourless eggs. The surface of the egg mass was partially covered with brownish lumps of detritus. The individual egg cell (fig. 120 B) measured 55—60 μ in diameter, i. e. it is a little smaller than those from the Isefjord (Rasmussen 1944) but much smaller than those from France (Pelseneer 1914) or from Frederikssund (see above). The water near Frederikssund is brackish, and it seems likely that the specimens from France have been studied near the mouth of one of the large rivers, i. e. also in brackish water. If so, the observations from the Isefjord and the Sound were made under the most marine conditions hitherto known. The 60 μ size of the eggs seems thus to be normal in water of a rather high salinity. — The egg cocoon is of the oval spindle-shaped type. A "calaza" from each pole of the egg cocoon is in direct connection with the neighbouring cocoons.

Evalea (Auriculina) insculpta (Montagu) (= **E. divisa** (J. Adams)). Northern part of the Sound, rare.

Reproduction: Unknown in the literature. No observations from the Sound. Judging from the apex (fig. 115 N) it seems probable that the development is non-pelagic or the larval life very short.

Parthenina indistincta (Montagu). Empty shells known from Hellebæk.

Reproduction: Unknown in the literature. No observations from the Sound. The apex (fig. 115 L) suggests a much reduced pelagic or an entirely non-pelagic development.

Parthenina interstincta (Montagu) (= **P. obtusa** (Brown)). Twelve living specimens known from clay bottom between Viken and Ellekilde.

Reproduction: Unknown in the literature. No observations from the Sound. The apex (fig. 115 M) supports the conjecture of a very short or a totally non-pelagic development.

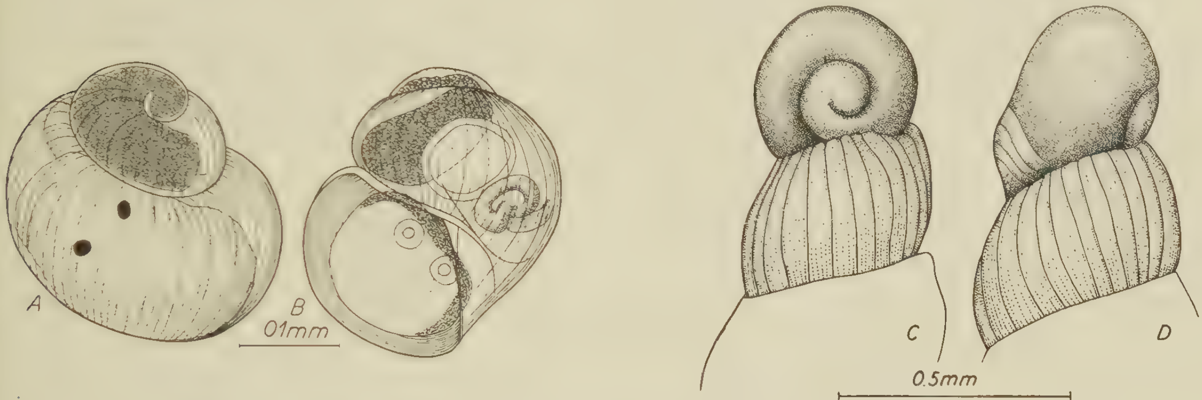


Fig. 121 A-D. *Pyrgiscus* (*Turbonilla*) *rufus* (Philippi). — *A* and *B*. Old larvae from plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{25}/_{10}$-1941 (drawn from life on $^{26}/_{10}$). Seen from the dorsal side (A) and the ventral side (B). — *C* and *D*. Apex of an adult specimen from the Kattegat (drawn from a specimen in the Copenhagen museum, "Hauch" St. 412). Seen from the top of the larval shell (C) and from the dorso-lateral side of the larval shell (D).

Partidula (Parthenia) spiralis (Montagu). Five living and one empty shells known from Hellebæk.

Reproduction: Pelseneer (1899a) has shown that this species is hermaphroditic. Eggs and development unknown. No observations from the Sound, but judging from the apex (fig. 115 Q) the species has a non-pelagic development or a shortened planktonic life.

Pyrgiscus (Turbonilla, Chemnitzia) rufus (Philippi). Northern part of the Sound, rather rare. Mr. P.-M. Lovén, Malmö Museum, has kindly informed me that the species has been found alive in dredge hauls between Höganäs—Nakkehoved and between Kullen—Kronborg, at a depth of 25 m.

Reproduction: A. Literature. Unknown.

B. Own remarks. The apex (fig. 121 C-D) bears a distinct sinistral, nearly globular larval shell, and the larva should accordingly be looked for in plankton, where it will occur as a sinistral, very tumid, nearly globular larva with a slightly elevated spire. Three larvae, which agreed with these conditions, were found off Helsingør on $^{25}/_{10}$-41 (fig. 121 A-B). The nearly globular shell ($2^1/_2$ whorls, height 295 μ, largest breadth 255 μ) was quite transparent. The yellowish-brown liver, the pale greenish stomach, and the two black eyes were seen through the shell. A purplish-blue border of pigment was seen along the inner margin of the operculum when the animal was retracted. No excretory organ could be discovered. The velum was quite colourless. The larva has never been seen in the plankton from Ven and seems to be rather rare in the Sound.

Eulimella acicula (Philippi) (= **E. commutata** (Monterosato)). Northern and middle parts of the Sound, rare.

Reproduction: A. Literature. Lebour (1932) figures the apex with the scalariform sinistral shell at the top.

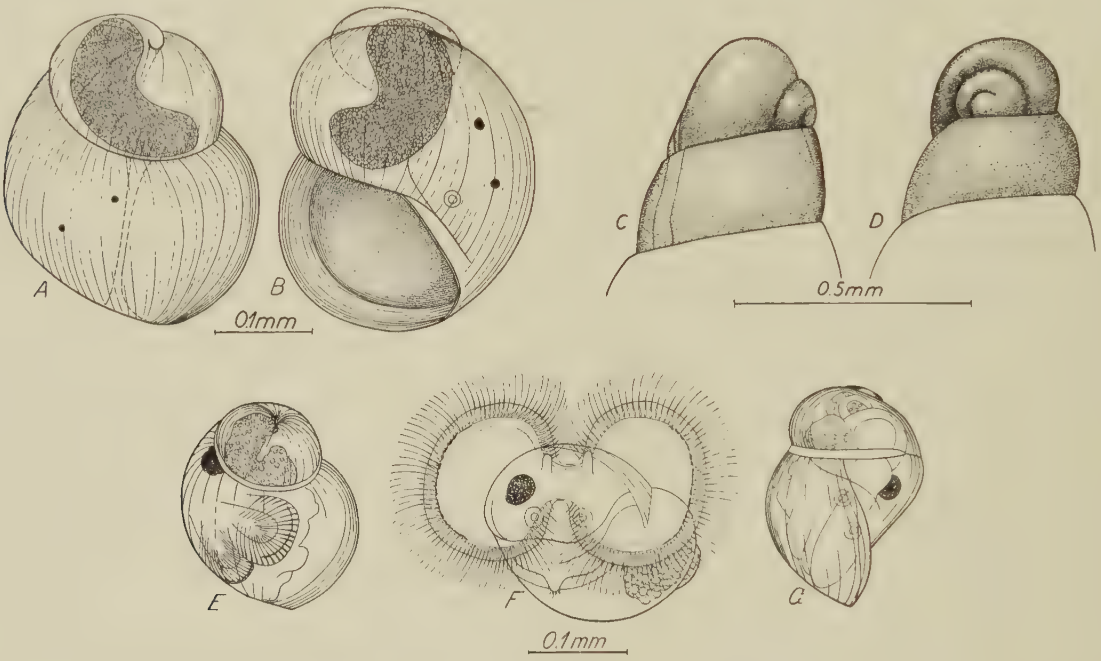


Fig. 122 A-G. *Eulimella acicula* (Philippi). — *A* and *B*. Old larva from plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{17}/_{9}$-1941 (drawn from life on $^{19}/_{9}$). Seen from the dorsal side (A) and the ventral side (B) with the animal withdrawn. — *C* and *D*. Apex of adult specimen taken 6 miles N. of Højen, depth 92 m (from a specimen in the Copenhagen museum). Seen from the dorso-lateral side of the larval shell (C) and from the top of the larval shell (D). — *E* to *G*. Young larva from plankton off Kristineberg (Bohuslän, Swedish W. coast), depth 40-0 m, on $^{24}/_{8}$-1945, (drawn from life on $^{25}/_{8}$). Seen from the dorsal side (E), the ventral side, swimming (F), and the left side (G).

B. Own remarks. Young larvae were obtained from Kristineberg plankton (Bohuslän, Swedish W. coast), depth 30—0 m, on $^{24}/_{8}$-1945. Here the adults are very common, and the larvae together with those of *Odostomia turrita* were the commonest *Pyramidellid*-larvae in the plankton. These young larvae (fig. 122 E-G) had colourless, transparent shells, 220 μ high and 175 μ broad, of about two whorls. An olive-green to bluish-grey liver, a reddish-brown excretory organ, and two distinct statocysts were present. The larvae had no eyes, a fact in good agreement with the very small eyes in older larvae. A swimming larva (fig. 122 F) shows a bilobed velum with long coarse cilia, the left lobe being the longer one. The outer part of each velar lobe has a brim of faint blackish-purplish pigment near the margin. The subvelum is distinct. The animal is yellowish-colourless.

The larval shell on the top of the apex (fig. 122 C—D) is rather tumid, with a short, somewhat depressed spire. A larva with a shell showing these characteristics was taken off Helsingør on $^{17}/_{9}$-41, and nine further larvae in all stages of development were found in the same locality on $^{7}/_{10}$-41. The larvae at hand (figs. 122 A—B) had transparent shells, a yellowish-brown liver, two small black eyes, but were otherwise quite colourless. The sealing-wax red excretory organs known from *Odostomia conoidea*, *O. acuta*, and *O. turrita* seemed to be absent. Statocysts were distinct. Height of larval shell 330 μ (the larval shell on the apex measures 315 μ), and largest breadth of shell 270 μ. The larva has never been found near Ven.

Eulimella nitidissima (Montagu). One living specimen recorded from Taarbæk. Probably often overlooked, owing to its very small size.

Reproduction: A. Literature. Erik Rasmussen (1944, pp. 215—220) has described and figured the egg capsules and embryonic development of this species from the Isefjord (Denmark): Breeding season May-August with a maximum in June. The gelatinous egg capsules, 3—4 laid at a time per animal (in aquaria), are rounded oblong, largest diameter 600—700 μ, and adhere to a substratum by a sticky surface. The individual egg capsule contains about 6—7 oval, opaque, pinkish eggs, largest diameter 100 μ, which at 22° C take five days to pass from fertilisation to hatching. The just hatched veliger, 125 μ across its shell, has a sinistral, oblique, clear and colourless shell with a typically "beaten" structure, a bilobed, colourless velum, black eyes, statocysts, and a larval kidney with reddish-yellowish pigment. The rather large velum and strong cilia seem to indicate a long pelagic life. — The same author (l. c.) figures the apex of an adult specimen from the Isefjord with a larval shell — 220 μ across — on the top.

B. Own remarks. The apex (fig. 123 D—G) is very characteristic, but the sinistral larval shell at the top has a quite different shape from that of the other larval shells within the Pyramidellids. The shape of the larval shell is nearly planorbiform, the first whorl being obtuse as compared with the following one. Thus we had to look in the plankton for a sinistral planorbiform larva with an obtuse first whorl. A single species of larva (fig. 123 A—C), agreeing entirely in appearence with the larval shell on the apex of *E. nitidissima*, occurred regularly, but in a few specimens only, in our plankton. The only difference between the planktonic larva and the larval shell on its apex is the size. The largest diameter of the planktonic shell was 430 μ; the largest diameter of the larval shell on the apex was only 220—230 μ. The apex figured here, however, is that of an English specimen, as it was the only specimen in the Copenhagen museum on which all details of the apex were distinct; in addition to this specimen the collections of the museum include specimens with more or less eroded apices, in which the diameter of the larval shell is much larger than in the British specimen figured here and in that figured by Erik Rasmussen from the Isefjord.

Finally, it proves to be very difficult to measure the exact diameter of the larval shell attached to the apex of the adults of this species, all the more so since the larval whorls are obtuse, and it is very likely that the last half or $^{3}/_{4}$ whorl of the free-swimming larval shell is so placed on the apex of the adults that it is taken for the first part of the adult shell and is not, therefore, included in the diameter of the "larval shell" when measured.

Nevertheless it can hardly be doubted that the larva is able to metamorphose in earlier or later stages in the different localities. Similar variations are known from other Mollusca, e. g. *Mytilus edulis* in different sea areas. As, moreover, no other Prosobranch exists in the Danish waters which has an apex like this one, there is no doubt whatever about its identity.

The larva in question (fig. 123 A—C) is planorbiform and sinistral. The obtuse apex is best seen from the umbilicus. The shell is transparent, the liver has a deep dark green colour in its hindmost part, the front part being yellowish-brown, often with a verdigris or navy-blue portion. The stomach has also a verdigris or navy-blue pigmentation, and the large excretory organ has a sealing-wax red colour characteristic also of other species of Pyramidellid larvae. The black eyes are very large, the statocysts distinct. The velum and the front part of the animal are quite colourless. — Younger larval stages (fig. 123 H, I) were sketched from Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40—0 m, on $^{12}/_{9}$-1945, and from the same date and locality a sketch of an old swimming veliger is at hand (fig. 123 K). — Young and medium-sized larvae are strongly photopositive.

The larva of *Eulimella nitidissima* is known from the plankton taken off Ven on: $^{19}/_{6}$-36 (1 spm.); $^{17}/_{10}$-36 (2 spms.); $^{1}/_{11}$-36 (a few spms.); $^{14}/_{11}$-36 (1 spm.); $^{6}/_{12}$-36 (2 large spms.); $^{9}/_{8}$-37 (1 large spm.); $^{12\text{-}13}/_{8}$-37; $^{12}/_{9}$-37 (3 spms.); $^{24}/_{9}$-37 (1 large spm.); $^{9}/_{10}$-37 (4 large spms.); $^{23}/_{10}$-37 (2 large spms.); $^{13}/_{8}$-38 (2 large spms.); $^{26}/_{8}$-38 (2 large spms.); $^{11}/_{9}$-38 (2 spms.); $^{24}/_{9}$-38 (3 large spms.); $^{8}/_{10}$-38 (1 spm.); $^{23}/_{10}$-38 (1 large spm.), and $^{18}/_{8}$-39 (1 large spm.), and off Helsingor on: $^{17}/_{9}$-41 (4 large spms.); $^{7}/_{10}$-41 (1 large spm.); $^{25}/_{10}$-41 (7 large spms.), and $^{17}/_{8}$-42 (2 large spms.). The main season is thus from August to December. PETERSEN (1888) mentions this species as an inhabitant of shallow water. The occurrence of the larvae in autumn plankton in the Sound seems to show, however, that in the Kattegat, the Sound, and the adjacent areas the species may live at larger depths also. As will be seen, only large larvae are found in the plankton of the Sound, and it is likely that they originate from parents in southern Kattegat and are carried to the Sound with the bottom current. The fairly great constancy and frequency of these larvae in our plankton suggest that the adults are much commoner than hitherto supposed, but that they have been overlooked owing to their small size.

Odostomia larva from the Limfjord (N. Jutland). In order to make known as many observations as possible on Pyramidellid larvae, it seems justifiable to mention and to figure here an *Odostomia* larva which I was able to sketch from plankton taken near Nykobing Mors during a visit there in the summer of 1940. Larvae of this type have never been met with in the Sound. The larvae (fig. 124 A—B), which had hardly attained their full size, had a height of the shell of 250 μ and 280 μ respectively. The shell showed nearly the same tumidity as that of *Odostomia acuta* (cf. fig. 117 A—B); there was a distinct suture along the base of each whorl, a very large sealing-wax red excretory organ, two large black eyes, and distinct otocysts. The liver, with rather fine globular bodies, was olive-green. The body was yellowish-white in direct light and transparent-colourless in transmitted light. The velar lobes were colourless and so was the foot. — Larvae of this type were not uncommon in plankton taken off Nykøbing Mors on $^{29}/_{6}$-40, horizontal haul in 2 m of water. It seems difficult to determine the exact identity. The absolutely dominant Pyramidellid species in the Limfjord is *Br. eulimoides*, but the apex of this (fig. 115 I) as well as the young larvae described by LEBOUR (1932) indicate that the larvae have a short pelagic life or a non-pelagic development. *Odostomia albella*, not uncommon in adult specimens in the Limfjord, is therefore most likely the parent of this larva. The apex of this species (fig. 115 C) bears a larval shell, which points to a long pelagic life, and the shape of the larval shell seems also to agree well with the larvae found. The larval shells on the apices, however, are much larger (about 390 μ high) than the larvae sketched from the plankton (250—280 μ high), which, however, may attain a much larger size before leaving the plankton. The exact identity of this larva is therefore still doubtful.

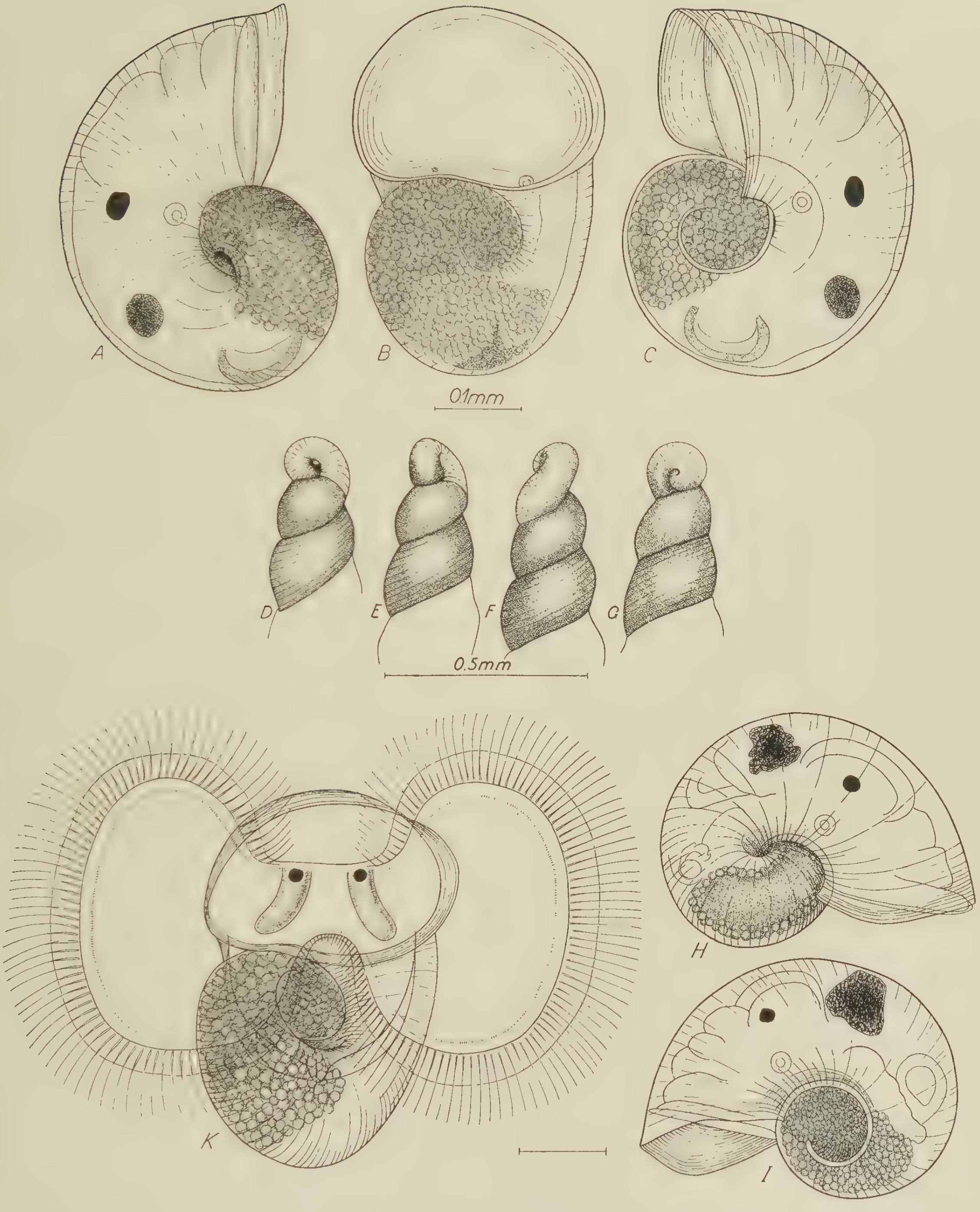


Fig. 123 A-K. *Eulimella nitidissima* (Montagu). — *A* to *C*. Old larvae from plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{17}/_{9}$-1941 (drawn on $^{18}/_{9}$). Seen from the umbilicus (A), the ventral side (B), and the top (C). — *D* to *G*. Apex of an adult specimen in different views (drawn from an English specimen in the Copenhagen museum). — *H* and *I*. Young larvae from Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40-0 m, caught and drawn from life on $^{12}/_{9}$-1945. Seen from the umbilicus (H) and the top (I). — *K*. Old swimming veliger, seen from the ventral side. Same locality and date as fig. H-I. — The scale between fig. K and I is 0.1 mm long.

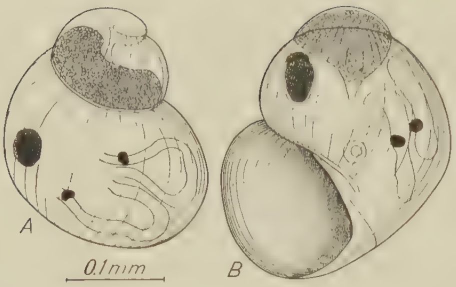


Fig. 124 A-B. Larvae of *Odostomia sp.* from plankton in the Limfjord (off Nykøbing Mors, NW. Jutland), depth 2-0 m, caught and drawn from life on $^{29}/_{6}$-1940. The larva possibly belongs to *Odostomia albella* LOVÉN (see the text on p. 210). — *A.* Medium-sized larva seen from the dorsal side. — *B.* Old larva seen from the ventral side.

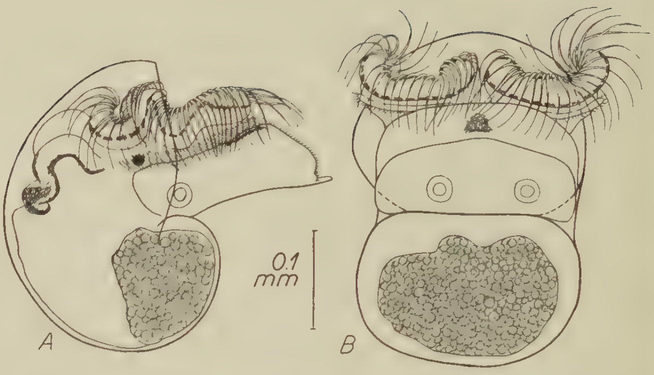


Fig. 125 A-B. *Crepidula fornicata* (LINNÉ). Planktonic larvae just hatched from the egg mass, seen from the right side (A) and from the ventral side (B). Nykøbing Mors (NW. Jutland), drawn from life on $^{4}/_{7}$-1940.

[**Crepidula fornicata** (LINNÉ). The species has been carried to the Limfjord (N. Jutland) with Dutch oysters (cf. SPÄRCK 1935), and is now of frequent occurrence in the western part of this area, viz. the area nearest the North Sea. — Unknown from the inner Danish waters (incl. the Sound).

Reproduction: A. Literature. CONKLIN (1891, 1897), ANKEL (1935, 1936 b), ORTON (1909, 1912, 1912—13, 1922), LEBOUR (1937 a) and several other authors have contributed to the study of the reproduction of this species, which may be summarised as follows: The protandric animals are normally arranged in "chains" with the small young male stages at the top, the larger hermaphroditic stages in the middle, and the oldest large female stages at the bottom. The eggs are laid in balloon-shaped capsules, 3.5 mm across "united in a branch by their stalks on a common stem fastened to a stone or shell and covered by the parent". The individual capsule, which is thin and cream-coloured, contains about 250 eggs, 160 μ across. Each egg floats in a fluid within its own membrane. About 70 capsules are laid by one single specimen. The veliger larvae have a bilobed velum, and the larvae have regular spots of pigment (green, red, brown, or black). The larval shell is spiral.

B. Own remarks. This species, now so common in the western Limfjord, will probably in the years to come spread to other Danish waters. Since during a stay at Nykøbing Mors in July 1940 I was able to sketch the larvae just hatched from the egg capsules, I consider it reasonable to publish the sketch here, although neither the larvae nor the adults are at present known from the Sound. -- The larva just hatched (fig. 125A—B) has a shell of $^{3}/_{4}$ whorl, 300—330 μ across, and of a broad, tumid appearance. There is no "beak" on the outer lip (pelagic life, therefore, hardly long). The slightly four-lobed velum has strong cilia, and two rows of reddish-purplish pigment along the margin. A subvelum is seen. The middle part of the intestine has characteristic black spots of pigment. Two black eyes, two statocysts. The stomach is filled with cream-coloured granules. The large ciliated foot has a triangular spot of black pigment in front. The shell is smooth and colourless, and so is the operculum. The green, red, brown, or black spots of pigment described for this larva by other authors (see above) were not observed in the newly hatched specimens, which — apart from the marginal pigment on the velum — were colourless. — Older larvae were not observed.]

Capulus hungaricus Linné. ?Gilleleje to Hellebæk, rare.

Reproduction: A. Literature. Brood protection, i. e. the egg cocoon is attached to the propodium of the mother animal, is mentioned by Jeffreys (1865), Lo Bianco (1888), and Odhner (1914a). Ankel (1936a) figures an animal, derived from Odhner's material, with the egg cocoon *in situ*, while Odhner had already (l. c.) figured the hatching veliger. Cerruti (1921) mentions brood-protecting females from Naples in March, and Lebour (1937a) has examined the whole development at Plymouth. The combined results of these authors may be summarised as follows: Breeding in March-April-May. Each female protects a single thin-walled cocoon of the form of a sausage, and each cocoon contains several eggs, 200 μ across, which hatch as veligers through a fissure on the under surface of the cocoon. The veligers are provided with *Echinospira* shells (cf. Lebour l. c., fig. 4d), 400 μ across, the true shell inside being 240 μ across. The *Echinospira* shell is almost spherical, transparent, gelatinous, covered with minute round spots arranged irregularly but tending to be radial. "The alimentary canal is very dark, the velum colourless and well developed". Long pelagic life.

B. Own remarks. This larva has not been recorded from the Sound. See, however, the remarks under *Velutina velutina*, pp. 222—224. An egg-cocoon taken under the foot of a Faroese specimen is figured here (fig. 126).

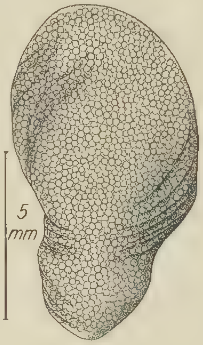


Fig. 126. *Capulus hungaricus* Linné. Egg cocoon taken under the foot of an adult female W. of the Faroes (62°16'5" N. 6°6" W.), depth 96-114 m, on $^{5}/_{7}$-1902 ("Michael Sars" St. 44). From a specimen preserved in alcohol and kept in the Copenhagen museum. The individual egg cocoon contains at least 5000 eggs.

Aporrhais pes pelecani Linné. Throughout the Sound, very common locally.

Reproduction: A. Literature. Lebour (1933a, 1937a) has described and figured the eggs and larvae from Plymouth. Breeding in late March to early summer. The eggs, laid singly or two or three together in the mud of the aquarium, were spherical, about 120 μ across the egg cell and 240 μ if the egg membranes are included. They form a thick tough coating, transparent and yellowish, with dirt on their surface. The young hatched prematurely, but older larvae are common in plankton. The youngest of them figured have "a four-lobed velum, with long lobes, each lobe with a large brown spot on the corner. The shell is smooth, 0.56 mm across, with a broad apex. The late larva has a six-lobed velum, each lobe having a large dark spot at the end and a dark brown border. The shell, about 1.4 mm across, has the last whorl beginning to be spirally striated". Two large tentacles are present. "At 1.5 mm it metamorphoses". The larvae remain long in the plankton.

B. Own remarks. Larvae of *Aporrhais* are rather common in the Sound, where they were taken off Ven on: July 1936 (common); August 1936 (a few large spms.); $^{2}/_{5}$-37 (1 spm.); $^{21}/_{6}$-37 (15 spms., several with a 6-lobed velum); $^{28}/_{7}$-37 (11 large spms.); $^{9}/_{8}$-37 (1 large spm.); $^{12-13}/_{8}$-37 (a few large spms.); $^{21}/_{8}$-37 (4 large spms.); $^{4}/_{9}$-37 (1 large spm.); $^{18}/_{4}$-38 (27 spms., in all stages); $^{10}/_{5}$-38 (4 large spms.); $^{18}/_{6}$-38 (1 large spm.); $^{1}/_{7}$-38 (1 spm.); $^{17}/_{7}$-38 (2 large spms.); $^{1}/_{8}$-38 (1 large spm.); $^{13}/_{8}$-38 (large spms.); $^{11}/_{9}$-38 (1 large spm.); $^{7}/_{1}$-39 (4 spms.); $^{25}/_{3}$-39 (2 large spms.); $^{10}/_{4}$-39 (8 large spms.); $^{17}/_{5}$-39 (16, in all stages); $^{4}/_{6}$-39 (7 medium-sized spms.); $^{17}/_{6}$-39 (13 spms., two of them large); $^{3}/_{7}$-39 (3 spms.); $^{15}/_{7}$-39 (3 spms.); $^{18}/_{8}$-39 (1 large spm.), and off Helsingør on: $^{25}/_{10}$-41 (6 large spms.); $^{11}/_{11}$-41 (20 spms., most of them very large); $^{2}/_{12}$-41 (2 spms.); $^{19}/_{12}$-41 (6 large spms.); $^{3}/_{1}$-42 (3 spms., one of them large);

$^{31}/_{1}$-42 (5 spms., some of them large); $^{10}/_{4}$-42 (4 medium-sized spms.); $^{15}/_{5}$-42 (17 young and medium-sized spms., the latter with 4 velar lobes); $^{4}/_{6}$-42 (3 medium-sized spms.); $^{20}/_{6}$-42 (5 young and medium-sized spms.); $^{6}/_{7}$-42 (56 medium-sized or large); $^{18}/_{7}$-42 (15 spms., quite young or very large, with 6-lobed velum); $^{25}/_{7}$-42 (7 spms. in all stages), and $^{17}/_{8}$-42 (1 medium-sized spm.). The main season for the occurrence of the larvae is thus from late March to early September. The winter larvae from 1941—42 seem to be derived from an extra spawning that year. The larvae are much more numerous off Helsingor than off Ven, and this in connection with the very high percentage of very large larvae makes it probable that the greater part of the larvae have been carried to the Sound with the bottom current from southern Kattegat.

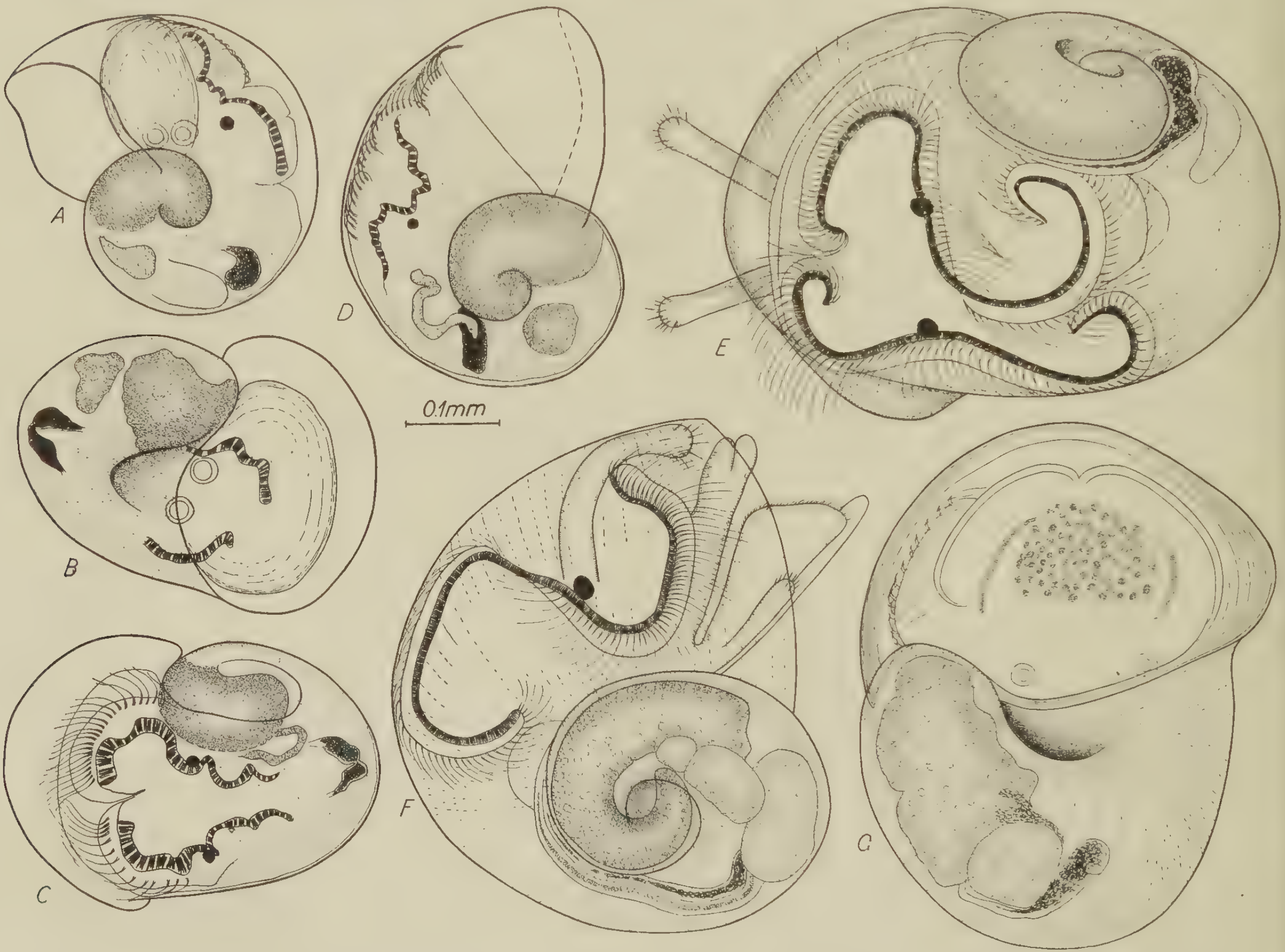


Fig. 127 A-G. *Aporrhais pes pelecani* LINNÉ. — *A* to *G*. Larvae from plankton off Ven, depth 18-0 m, drawn from life on the day of capture. — *A* to *D*. Young larvae, caught on $^{7}/_{1}$-1939, seen from the left side (A), the ventral side (B), the dorsal side (C) and the right side (D). — *E* to *G*. Oldest planktonic larvae found ("swimming-crawling" stage) just before metamorphosis. Caught on $^{2}/_{7}$-1943, seen from the dorsal side crawling on the object-glass (E), the right side (F) and the ventral side (G).

The larvae (fig. 127, 128 A-B) may or may not have spots of pigment at the end of each velar lobe, even in the six-lobed stage. Fig. 128 A shows a six-lobed larva from Frederikshavn (N.W.

Kattegat) with a reddish-brown rim of pigment along the margin and reddish-brown pigment on the foot, but without any pigment spots on the velum; quite similar stages were found at Frederikshavn on $^{30}/_{7}$-39 and in the Sound on $^{25}/_{7}$-42. Fig. 128 B shows a larva from the Gullmarfjord (Swedish W. coast) in a similar stage of development but with distinct dark-purplish spots on the corner of the velar lobes and a reddish-brown border along the margin. Occasionally, however, we also observed four- and six-lobed larvae in the Sound with spots of pigment on the velum, but those without spots were in the majority. The young larval stages (fig. 127 A-D) are characteristic owing to their broad, flat whorls, their yellowish-brown liver, and the black-pigmented part of the intestine. – The bottom stages just after metamorphosis (fig. 128 C-D) have a height of the shell of 1080 μ, and are characterised by the flat apex, the nearly globular shell, and the reddish-purplish beak-like canal. The last whorl has a spiral striation. Gills, intestine, and the olive-green liver are visible through the shell. Purplish-black pigment is found on the dorsal side of the foot below the operculum.

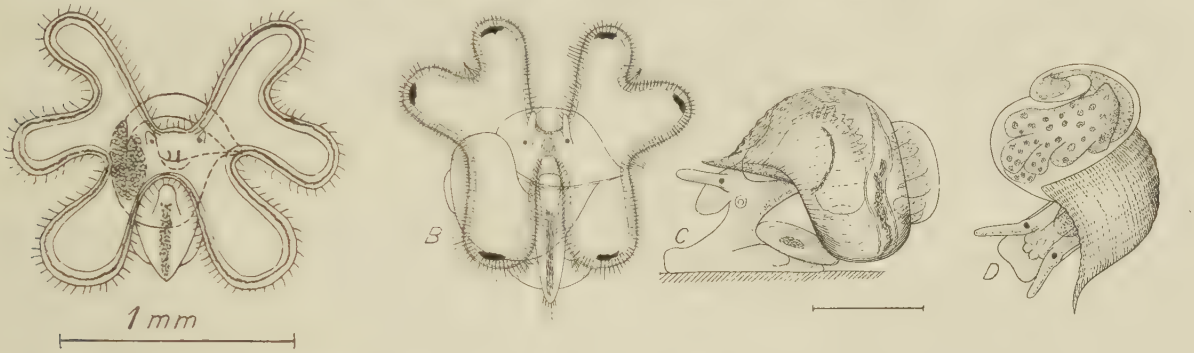


Fig. 128 A-D. *Aporrhais pes pelecani* LINNÉ. — *A*. Old larva swimming in the water. The velum, though six-lobed, shows no traces of the pigment spots described from English specimens. Off Frederikshavn, NW. Kattegat, depth 8-0 m, caught and drawn from life on $^{3}/_{7}$-1937. — *B*. Veliger larva in the same stage with dark-purplish spots on the corner of each velar lobe. From plankton off Kristineberg (Bohuslän, Swedish W. coast), depth 30-0 m, caught and drawn from life on $^{24}/_{8}$-1945. — *C* and *D*. Bottom stage just after metamorphosis, seen from the left side (C), and from the dorsal side (D). From plankton off Kristineberg, depth 40-0 m, caught and drawn from life on $^{22}/_{8}$-1945. Scale for B-D 0.5 mm.

Amauropsis islandica (GMELIN). A half-grown living specimen was taken on $^{8}/_{7}$-42 off Knähaken (northern part of the Sound), depth 25—35 m, in a *Modiola* epifauna.

Reproduction: A. Literature. Egg masses described and figured by THORSON (1935 a) from East Greenland. The egg band is of the shape typical of the genus *Natica*. The individual egg space is 1500—1750 μ across, and a single egg band consists of 150 -200 egg spaces. Each egg space contains one egg only, which is oval with the longest diameter 1500 μ. The largest embryo found had a length of 750 μ and was still surrounded by a considerable mass of white. The species has no pelagic stage.

B. Own remarks. Nothing is known about the reproduction from the Sound.

Natica (Lunatia) pallida BRODERIP & SOWERBY. Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. The egg masses described and figured by THORSON (1935 a) from East Greenland are of the common type found in all species of *Natica*. In this species, however, the individual egg spaces are very large, 2500—3000 μ across; 40—50 egg spaces seem to be the largest number per egg mass. The egg membrane, 2250 μ across, contains a single embryo surrounded by a considerable quantity of white. The embryos develop within the egg mass into young snails, which, when hatching, are closely similar to the adults, and the largest breadth of the shell is 1700 μ. The velum is reduced long before the young hatch out; thus the species has no pelagic stage.

B. Own remarks. From the dredgings made off Helsingør in 1941 to 1942 a number of about 35 egg masses of this species were examined (fig. 129A). They were taken between $^{7}/_{7}$-41 and $^{11}/_{11}$-41 and between $^{15}/_{5}$-42 and $^{10}/_{7}$-42 (last dredge hauls were made on $^{18}/_{7}$-42, but no egg masses were found). The egg mass from $^{15}/_{5}$-42 contained fairly old embryos; those from July to September contained eggs and young in all stages of development, and those from $^{11}/_{11}$-41 contained veligers which were very probably liable to remain for at least a fortnight more inside the egg mass before hatching. The spawning season is thus rather long, at least from April to November, and as the number of dredge hauls made in the spring of 1942 was very small, the egg capsules have probably been overlooked on earlier dates. — Normally each egg space contains one egg or embryo only (fig. 129B), but a single egg mass from $^{14}/_{7}$-41, which corresponded closely to the others in external appearance, contained twin-embryos in young veliger stages in all the egg spaces (fig. 129C—D). In such cases, which seem to be very rare, where twin-embryos have to feed on the same lot of white which is normally devoured by one embryo only, the embryos may hatch already in the veliger stage and may then have a short pelagic life in the plankton. However, such larvae were not met with in the Sound.

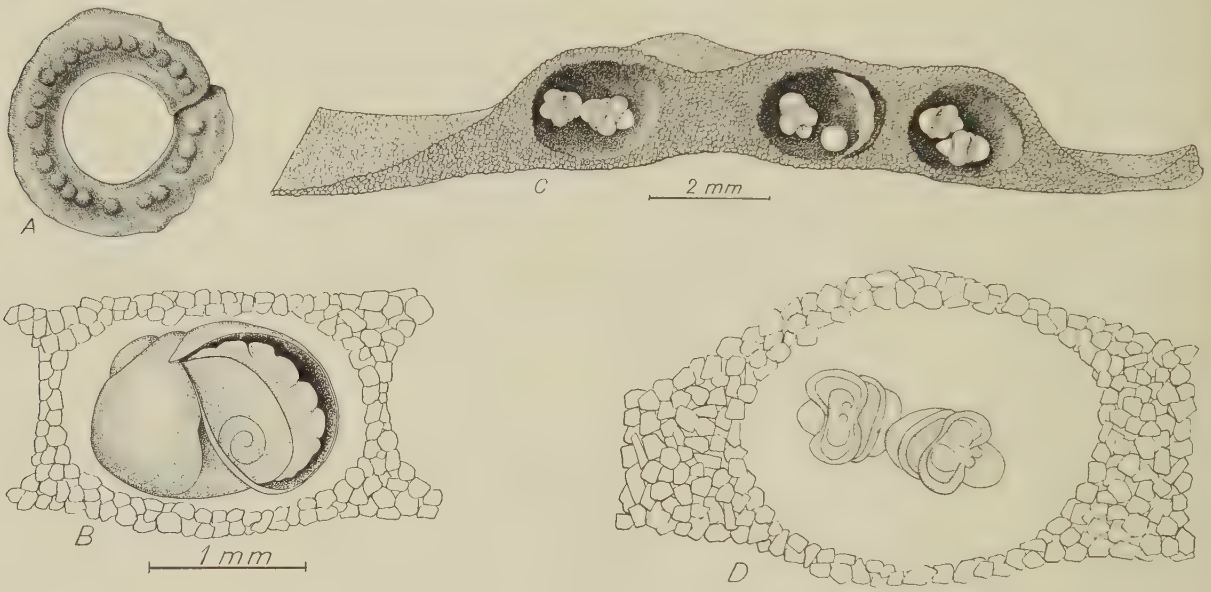


Fig. 129 A-D. *Natica* (*Lunatia*) *pallida* BRODERIP & SOWERBY. — *A*. Egg ring with a single row of egg-spaces taken off Hellebæk, depth and date unknown. Seen from above. — *B*. Transverse section of egg space with a large embryo ready to hatch. Off Hellebæk, depth 30 m, caught and drawn from life on $^{14}/_{7}$-1941. — *C*. Transverse section of large egg mass with three rows of egg spaces containing twin embryos. The egg space in the middle contains one undeveloped egg, one embryo, and a remnant of the white-like stuff on which the embryos feed. Locality, date and depth as in fig. B. — *D*. Section of a single egg space with twin embryos from the egg mass fig. C.

Natica (Lunatia) nitida DONOVAN (= **N. pulchella** RISSO = **N. intermedia** PHILIPPI). Northern part of the Sound, rare.

Reproduction: A. Literature. JEFFREYS (1867) has briefly mentioned the egg masses of this species, which together with the larvae have been described and figured by HERTLING (1932 b) from Heligoland. LEBOUR (1936, 1937 a) describes the eggs and late larvae from Plymouth. Breeding at Heligoland (in aquaria) from October to January. The flattened spawn is "usually forming an incomplete slightly spiral sandy ring, about 25 mm across and 7—8 mm wide". The individual egg space, 240 μ across, contains a single small egg, 160 μ across, which develops into a veliger and hatches about 3 weeks after having been spawned. The larvae hatched figured by HERTLING (l. c.), however, are not normal; under natural conditions the larvae will hatch as veligers with a well developed spiral shell (see below). LEBOUR (l. c.) refers with some doubt late larvae from the Plymouth plankton to this species. These very large larvae have smooth transparent shells of about $3^1/_2$ whorls, the shells being 800—1000 μ across. Velum four-lobed, very large, "the lobes being drawn out each with a large round spot in the end". The late larva is thus very like that of *Nassa incrassata,* but has no beak-like process on the outer lip.

B. Own remarks. On the large sandy areas off Frederikshavn (N.W. Kattegat), depths 10 to 12 m, adults as well as egg capsules of this species were abundant in July 1936. Several egg masses (like that fig. 130 A) were placed in aquaria here and the larvae hatched out. In an egg mass taken on $^{14}/_7$-36 (fig. 130 B) and placed in a glass dish the embryos hatched out on $^{22}/_7$-36. The hatching embryos (fig. 130 C-E) have normal spiral shells and a much more advanced organisation than the newly hatched larvae from Heligoland figured by HERTLING. On $^{23}/_7$-36 another spawn was secured, and the young larvae, which hatched on $^{24}/_7$-36, i. e. hardly 24 hours after the capture, had precisely the same appearance as those reared in aquaria at Frederikshavn. Thus the newly hatched larvae from Heligoland must be regarded as abnormal, probably influenced by their long stay in the aquarium.

The normal larval development is that shown in fig. 130 C-I. The hatching larva has a colourless transparent shell, 195 μ across, with a brownish-black columella. The whole surface of the embryonic shell is covered with fine, wavy spiral lines forming a pattern which I have never found again on the apex of any other larval Prosobranch in the Danish waters. The spiral lines are much more closely packed than those of the *Rissoa sarsi* and the *Alvania* larvae (cf. these species). The whole larva is colourless, with a bilobed velum and pale greyish contents of the stomach. Two black eyes, two distinct statocysts. The larva three days old (fig 130 D-E) has precisely the same appearance, and the mouth is distinctly seen. Larvae five days old (fig. 130 C) have a distinct larval heart, and an oval organ with a few scattered grains of carmine (probably the excretory organ) is seen through the shell. Now the shell begins to grow, and the new part of the whorl is smooth, the spiral structure thus being restricted to the shell formed within the egg mass (fig. 130 D-F). In July 1936 young as well as older larvae were found in plankton hauls taken across the sandy areas off Frederikshavn. The larva (fig. 130 G) has more than half a smooth whorl, the velum is now four-lobed, and each lobe has a large dark purplish spot of pigment at the end. The still older larva (fig. 130 H) has two large tentacles, a yellowish-brown liver, and a very large operculum of the shape and spiral-growth characteristic of the genus *Natica*. The smooth part of the shell (nearly $^3/_4$ whorl) is colourless, transparent, and with a very conspicuous fatty lustre. The pharynx has a few dark grains of pigment. The shell of larvae in this stage is 360 μ across. — Fig. 130 I shows a swimming veliger, 750 μ across the shell, which is the oldest larval stage known from our seas

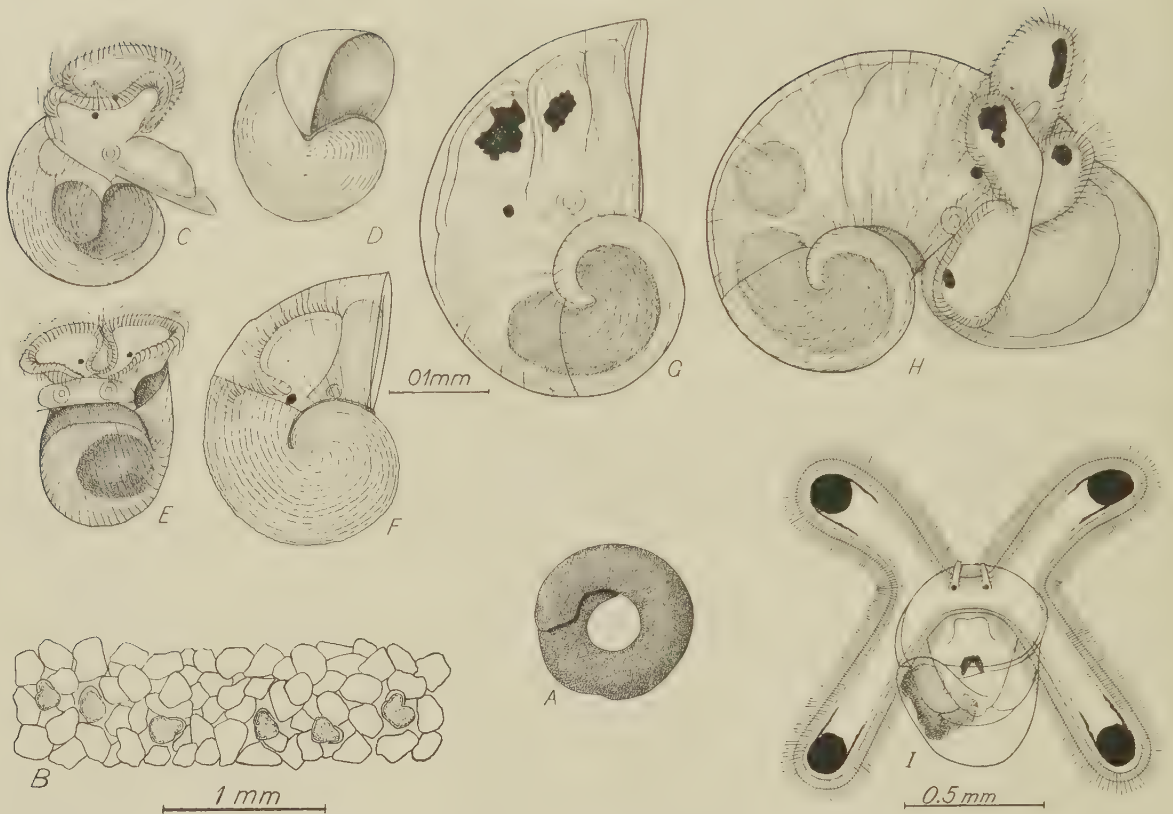


Fig. 130 A-I. *Natica* (*Lunatia*) *nitida* Donovan (= *N. pulchella* Risso). Egg mass and development. — *A*. Egg mass from Skagerrak, depth 25 m, taken on $^{18}/_{6}$-1934 (from a fixed egg mass in the collection of the Göteborg museum, seen from above, natural size). — *B*. Transverse section of egg mass taken off Frederikshavn (NW. Kattegat), depth 10-12 m, on $^{14}/_{7}$-1936 (drawn from life on $^{15}/_{7}$). Six embryos with cup-shaped shells are seen. — *C* to *E*. Larvae hatched in aquaria from egg masses taken off Frederikshavn, depth 10-12 m, sand bottom. — *C*. Seen from the right side, velum distended (from egg mass taken on $^{23}/_{7}$-1936, larva hatched on $^{24}/_{7}$ and drawn from life on $^{29}/_{7}$). — *D*. Empty shell a few days after hatching with the first part of the smooth larval shell formed. — *E*. Larva with distended velum seen from the front (from the egg mass fig. B, three days after hatching). — *F*. Larva of medium size with the animal withdrawn. Seen from the right side. From plankton off Ven, depth 18-0 m, caught and drawn from life on $^{25}/_{8}$-1939 (sketch by stud. mag. Erik Rasmussen). — *G*. Old larva from plankton off Frederikshavn, caught and drawn from life on $^{31}/_{7}$-1936. Seen from the right side. Animal withdrawn. — *H*. Medium-sized larva with the velum distended. From plankton off Frederikshavn, depth 3-0 m, caught and drawn from life on $^{31}/_{7}$-1936. Seen from the right side (drawing rather bad since the velum as well as the foot and operculum were somewhat squeezed under the covering glass). — *I*. Oldest pelagic stage, swimming, seen from the ventral side. From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 40-0 m, caught and drawn from life on $^{23}/_{8}$-1945.

(from plankton in the Gullmarfjord, Swedish W. coast). The velum as well as the shell closely resemble those figured by Lebour (1936, pl. II, figs. 28—29) and supposed by her to belong to the species in question. The foot may or may not have greyish-black pigment in the middle. Lebour gives no information about the spiral-structured embryonic shell.

Larvae of this type were met with off Ven on: $^{21}/_{8}$-36 (1 large spm.); $^{26\text{-}27}/_{9}$-36 (2 large spms.); $^{18}/_{12}$-37 (1 large spm., just as fig. 130 H); $^{25}/_{8}$-39 (1 large and 1 young spm., fig. 130 F), and off Helsingør on: $^{25}/_{7}$-42 (1 young spm.), and $^{5}/_{9}$-42 (1 half-grown and 2 young spms.). The main season is thus summer and autumn; the larvae are rather rare, but the very young stages found seem to confirm that at least some of them originate form the Sound itself.

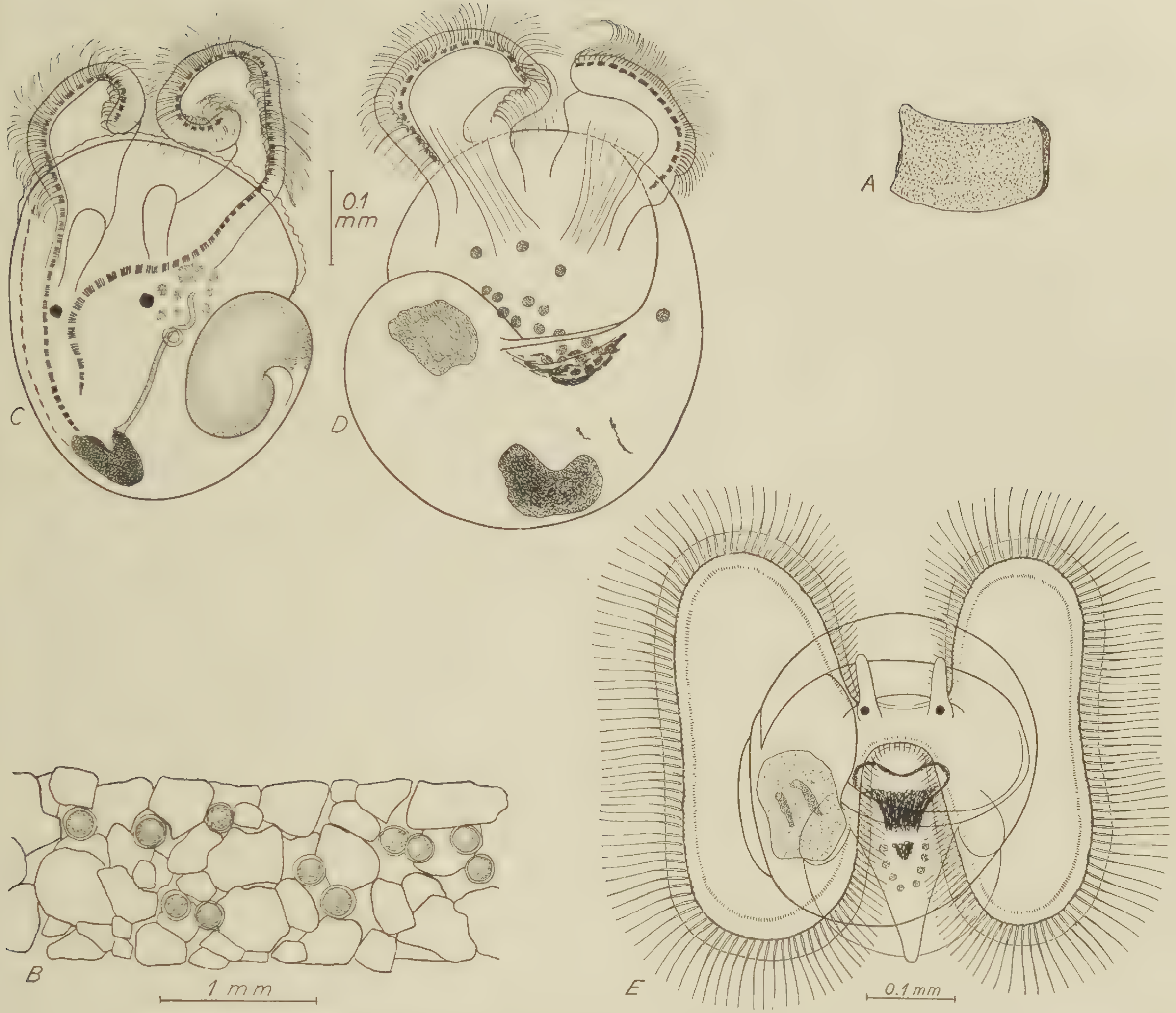


Fig. 131 A-E. Egg masses and planktonic larvae belonging to *Natica* (*Lunatia*) *montagui* Forbes (see the text on pp. 219-220. — *A.* Piece of egg ring taken between Hellebæk and Sofiero, depth 35 m, hard sand bottom with shells, on $^{8}/_{7}$-1941 (natural size). — *B.* Transverse section of the egg ring fig. A, drawn from life on $^{9}/_{7}$-1941. — *C* and *D.* Old larvae from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{25}/_{9}$-1938. Seen from the dorsal side (C) and the ventral side (D). The velum is only partially streched out. — *E.* Larva of medium size, swimming, seen from the ventral side. From Gullmarfjord plankton (Bohuslän, Swedish W. coast), 40-0 m, caught and drawn from life on $^{11}/_{9}$-1945.

Natica (Lunatia) montagui Forbes. Northern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. Unknown.

B. Own remarks. From the plankton found in the Sound and N.W. Kattegat large larvae are at hand, which in the shape of the shell as well as in the type of the operculum bear such close similarity to the young crawling stages of for instance *Natica pallida* and *Natica affinis* (cf. Thorson 1936, figs. 61 & 63) that their reference to the genus *Natica* can hardly be questioned. The only species of *Natica* found in the inner Danish waters which can be regarded as the parent, is *Natica montagui. Natica catena* has been thoroughly investigated at Frederikshavn, where the larval development always seems to be non-pelagic. Moreover, this latter species has never been taken in the Sound nor in eastern Kattegat, and other species than those mentioned here and above are not known from our seas. The distribution of the adult *Natica montagui*, viz. in the Mediterranean and in the lusitanian and boreal parts of the North Atlantic (just like that of *N. nitida*) seems also to suggest a pronounced pelagic larval development.

These larvae (fig. 131 C—D) always attain a very large size in the Sound. The youngest stages seen were 320—350 μ across the shell, and the largest larvae found measured up to 550—650 μ. The shape of the shell and of the animal was the same in these two sizes. The shell was globular with a distinct beginning of an umbilicus, enamel-white with a cream-coloured apex in direct light, colourless and transparent in transmitted light. The liver was reddish-brown, the intestine had in its curvature an intense bluish-black pigmentation. Two black eyes, distinct otocysts, and two large tentacles. The velum had two rounded lobes and a brownish-black border of pigment along the whole margin. Spots of pigment on the velum have never been seen. When the larva was withdrawn in its shell there was a deep black pigmentation in the region round the umbilicus; the body contained a large, rounded organ (probably the excretory organ) of a mahogany-brown colour. On the foot close to the operculum were some large spots, which were yellow in direct light. Observations on the swimming larva (fig. 131 E) showed that the black and yellow pigment visible through the shell was found on the propodium and on the foot. The foot further has two characteristic lateral lobes. The velum is bilobed. The operculum had the spiral lines of growth so characteristic of the genus *Natica*, and the larvae ready to metamorphose (fig. 131 C—D) agreed so well with the young stages of *Natica montagui* that their identity seems rather certain. Our larvae are so similar in size, shape, and pigmentation to those referred by Lebour (1936, p. 558, figs. 26 and 27) to *Natica catena* that Lebour's identification must be questioned (see this paper p. 222).—Young and medium-sized larvae are photopositive.

On the sea bottom between Hellebæk and Sofiero, depth 35 m, hard sand and shells, a fragment of an egg ring belonging to the genus *Natica* (fig. 131 A) was taken on $^{8}/_{7}$-41. This egg ring was nearly of the same type as the egg mass of *Natica nitida*, but it was somewhat broader and of a more solid structure. A transverse section (fig. 131 B) showed that the eggs were arranged along more than one plane and thus differ from the conditions normally found in *N. nitida* (fig. 130 B). As the egg masses of all the other species of *Natica* occurring in the inner Danish waters are well known, it seems reasonable to refer this egg mass to *Natica montagui*, though nothing definite can be stated. The individual egg space measured about 230 μ across, and the egg itself about 150 μ across. The eggs were in the first stages of development.

Larvae of *N. montagui* were present in the plankton taken off Ven on: $^{18}/_{9}$-36 (2 large spms.); $^{26\text{-}27}/_{9}$-36 (1 spm.); $^{6}/_{12}$-36 (8 large spms.); $^{9}/_{10}$-37 (8 large spms.); $^{25}/_{9}$-38 (9 large spms.); $^{18}/_{8}$-39 (1 large spm.); $^{16}/_{9}$-39 (12 medium-sized or large spms.), and off Helsingør on: $^{17}/_{9}$-41 (5 large spms.); $^{7}/_{10}$-41 (13 spms., most of them large); $^{25}/_{10}$-41 (2 medium-sized spms.); $^{19}/_{12}$-41 (1 large spm.), and $^{5}/_{9}$-42 (1 large spm.). Main season: late August to early September. The dominance of the large specimens suggests that most of the larvae originate from southern Kattegat and are carried into the Sound by the bottom currents.

[**Natica catena** (da Costa). Unknown from the Sound, the Baltic, and Eastern Kattegat. Common in N.W. Kattegat, the Skagerrak, and the North Sea.

Reproduction: A. Literature. Jeffreys (1867, p. 213) describes the spawn and states that the embryos spend at least two months inside the egg spaces. Hertling (1932 b) gives

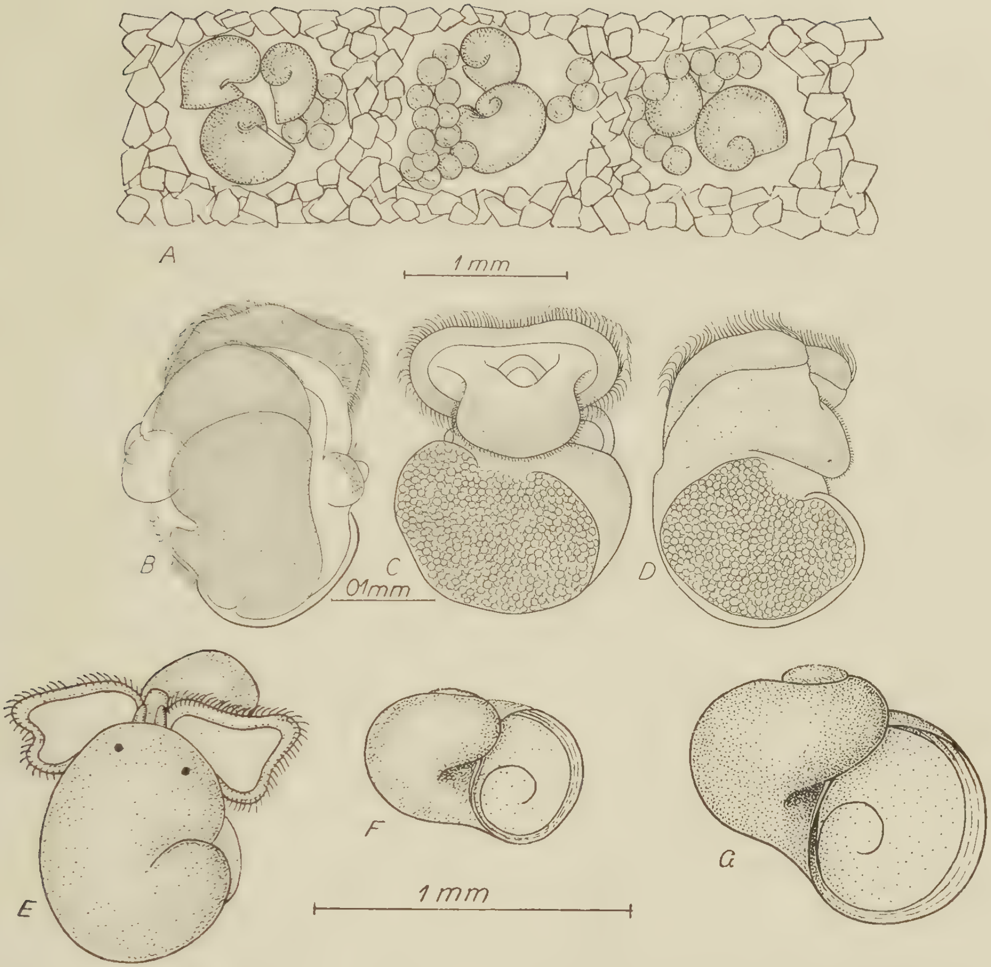


Fig. 132 A-G. *Natica catena* (Da Costa). — *A.* Transverse section of egg mass showing three egg spaces with large embryos and nurse eggs. Taken in Kattegat on $^{29}/_{6}$-1913 (from a specimen in the Copenhagen museum, fixed in alcohol). — *B.* Young Veliger from an egg space with four rotating embryos and 19 nurse eggs. Taken off Frederikshavn (NW. Kattegat), depth 10-12 m, on $^{14}/_{7}$-1936, (drawn from life on $^{15}/_{7}$). Seen from the ventral side. Velum, foot, larval heart, excretory organ and the first traces of shell are seen (compare the figure of Hertling (1932, p. 100) of the *Natica nitida* larva). — *C* and *D.* Somewhat older Veligers which, dissected out from the egg mass and placed in glass dishes with sea-water, moved actively about for several days. From egg masses taken off Frederikshavn, depth 9 m, on $^{7}/_{7}$-1937 (drawn from life on $^{8}/_{7}$). Seen from the ventral side (C) and from the right side (D). — *E.* Late Veliger which, when dissected out of the egg space, was able to crawl rapidly along the bottom of a glass dish. Taken off Frederikshavn, depth 12 m, on $^{23}/_{7}$-1936 (drawn from life on $^{24}/_{7}$). — *F* and *G.* Smallest and largest embryos ready to hatch from the same egg mass, both non-pelagic. Taken off Frederikshavn, depth 12 m, on $^{23}/_{7}$-1936 (drawn from life on $^{24}/_{7}$).

good figures of the egg masses from Heligoland. Ankel (1930) describes the nurse egg feeding of this species from Heligoland as follows: Each of the globular egg spaces contains a few embryos (about 3 or 4) and several eggs (about 50) cleaving in an atypical way and serving as food for the normal embryos, which were seen with eggs in their intestines. Ankel gives no information about the stage (pelagic or non-pelagic) at which the larvae hatch from their egg spaces. Lebour (1936, p. 558, pl. II, figs. 26 and 27) describes and figures larvae from Plymouth plankton, which she attributes with some doubt to this species. The shell of the late larva is 480 μ across, globular, smooth and transparent with two and a half whorls and a wide mouth without siphon. Velum bilobed with a purple-brown border. Animal yellowish-white with two large tentacles. — Breeding season at Plymouth in spring.

B. Own remarks. Although this species is unknown from the Sound and the adjacent areas, I take the opportunity to mention here some observations made in other Danish waters. At Frederikshavn (N.W. Kattegat), the Skaw and the northern North Sea 21 egg masses (fig. 132 A) have been examined. The number of eggs per egg mass has been counted for 20 egg spaces, and the average results have been calculated. The egg spaces have a diameter of from 1200—2000 μ (average 1600 μ), and each egg space contains 25 to 110 (average 62) eggs and embryos. The average number of embryos per egg space in our seas is 1 to 4, mostly 2 to 3, and only very rarely up to 6 or 7 embryos are met in the individual egg space. In all the cases hitherto examined from our seas the embryos seem to hatch with a shell quite like those of the adults and without any pelagic stage at all. The embryos ready to hatch may vary considerably in size, but seem always to have passed the Veliger stage before hatching (fig. 132 F—G). Egg masses from Heligoland seem to contain a somewhat larger number of embryos per egg space (of average size), thus for three egg masses examined 3.5, 4 and 8 embryos on an average per egg space. Hence we cannot exclude the possibility that the embryos are able to hatch as pelagic larvae in the southern part of the area in which the species occurs.

Accordingly, the pelagic larvae referred by LEBOUR to this species (see above) may belong to *Natica catena*, although this species has a non-pelagic development in our seas. The larvae figured by LEBOUR show, however, the closest similarity in size, shape, and pigmentation to those of *Natica montagui* described from the Sound (see this paper pp. 219—220, fig. 131 C—D). Their identity with this species, which has a wide boreo-lusitanian distribution and is known to occur at Plymouth (JEFFREYS 1867, p. 228), seems therefore much more reasonable. If I am correct in identifying LEBOUR's larvae with *Natica montagui*, the pelagic larvae of *N. catena*, if any, are thus still unknown.]

Velutina velutina (O. F. MÜLLER). Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. LEBOUR (1935 b, 1937 a) describes and figures the larva of *Velutina velutina*. The eggs are not known. The larva is a typical *Echinospira*. The outer shell — the *Echinospira* shell — is nautiloid, globular, gelatinous "of little more than one whorl, usually more or less covered with minute debris; small dots radiate from near the centre, probably being pores from which mucus exudes". The smallest larvae seen measured 960 μ across the *Echinospira* shell (350 μ across the quite smooth true shell). The oldest larvae found had *Echinospira* shells measuring 1400—2000 μ across, and the true shells (640—1280 μ across of up to three and a half whorls) were provided with four to five longitudinal ridges running outwards towards the mouth, and "two layers in the shell are conspicuous". The velum is bilobed at first, later on faintly four-lobed, quite colourless. Reared through metamorphosis at Plymouth, where the species has been found in plankton in the late spring and summer.

B. Own remarks. BERGH (1880—1887) has described and figured larvae from egg capsules laid in sponges and referred by him to *Onchidiopsis groenlandica*. He states that no *Echinospira* shell exists, but his figure, pl. Z figure 17, contradicts his words. His only reason for identifying these larvae with *Onchidiopsis* is that the sponge was sent to the Copenhagen museum together with three specimens of *Onchidiopsis*. — In the Sound plankton *Echinospira* larvae were taken off Ven on: $^{30}/_{4}$-39 (1 larva, 485 μ across the *Echinospira* shell, 350 μ across the true shell); $^{17}/_{6}$-39 (1 larva, 1120 μ across the *Echinospira* shell, 700 μ across the true shell); $^{1}/_{7}$-43 (1 larva, 1300 μ across the *Echinospira* shell, 840 μ across the true shell, fig. 133 D–E); off Helsingør on: $^{12}/_{4}$-42 (1 larva, 560 μ across the *Echinospira* shell, 430 μ across the true shell, fig. 133 A—C); $^{4}/_{6}$-42 (1 larva quite similar to that from $^{12}/_{4}$-42 in shape, colour, and size), and off Snekkersten on $^{19}/_{5}$-1928 (1 larva, 1580 μ across the *Echinospira* shell, 980 μ across the true shell).

All the specimens of *Echinospira* seemed to belong to one and the same species. The younger stages (fig. 133 A—C) had an *Echinospira* shell which was similar in all details to the larval shell figured by BERGH (l. c., pl. Z, fig. 17) and referred by him to *Onchidiopsis*. Our larvae, however, seem to be somewhat older than those taken from the egg capsules and figured by BERGH. While in his specimens the whole larval shell has a spiral striation, the spirally striated part of the shell in our larvae continues in a soft, gelatinous, quite smooth and still more globular shell, forming the next part of the whorl. In older larvae (fig. 133 D—E) this gelatinous whorl entirely covers the oldest, striated part of the *Echinospira* shell, which is now very difficult to distinguish. In the younger larvae the true larval shell is quite smooth, in the older larvae it is provided with longitudinal ridges (fig. 133 E). The velum in the young specimens was provided with a dark reddish-brown border of pigment, and a similar pigmentation was seen on the foot in older stages. The stomach in young specimens has a brownish-black pigmentation, and a pale greenish liver; two distinct statocysts were seen, but no eyes. The older larvae (fig. 133 D—E) have a yolk-coloured liver, a broad purplish-brown band of pigment on the velum, a faintly purplish stripe of pigment along the mantle border, two small black eyes, one distinct statocyst, and greyish-black contents of the rectum. The *Echinospira* shell is quite colourless and so transparent that it is difficult to detect when the larva is seen in transmitted light.

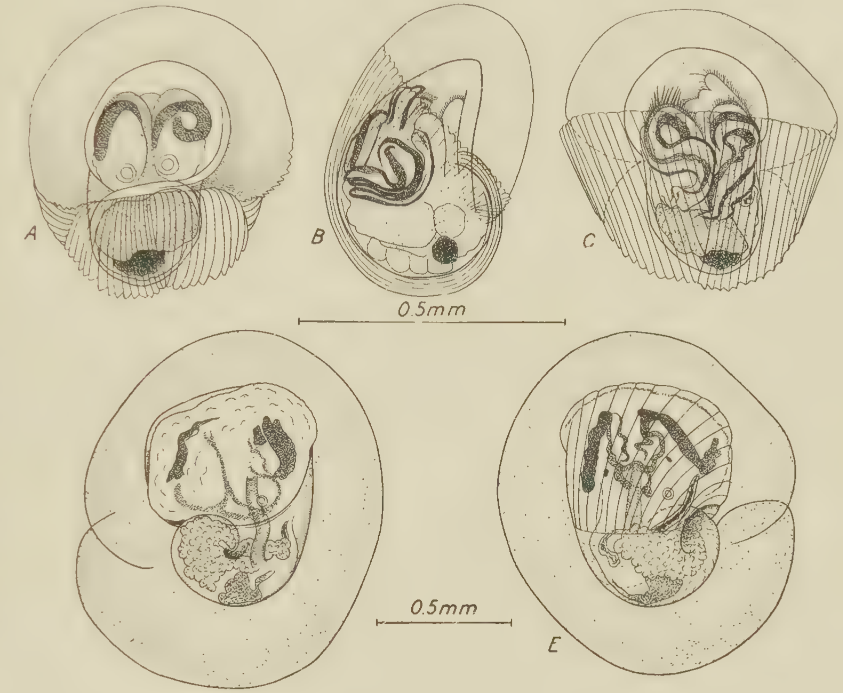


Fig. 133 A-E. *Velutina velutina* (O. F. MÜLLER). Planktonic larvae. — *A* to *C*. Young larva with structureless inner shell and structure upon the *Echinospira*-shell. The animal is withdrawn. Seen from the ventral side (A), the right side (B), and the dorsal side (C). Taken in plankton between Hellebæk and Kulla Gunnarstorp, depth 35-0 m, on $^{10}/_{4}$-1942 (drawn from life on $^{12}/_{4}$). — *D* and *E*. Older larva with structure upon the inner shell and a gelatinous, structureless *Echinospira*-shell. The animal withdrawn. Seen from the ventral side (D), and the dorsal side (E). Caught in plankton off Ven, depth 18-0 m, on $^{1}/_{7}$-1943 (drawn from life on the same day).

The similarity to the "*Onchidiopsis* larva" of BERGH is very pronounced. Also the sizes of the *Echinospira* shells agree fairly well (BERGH's larva 0.6 mm across, our larva 0.56 mm across in the same stage of development). It is quite impossible, however, that the larvae from the Sound should be referred to *Onchidiopsis*, as this genus is entirely absent from the Danish waters. Owing to the rather common occurrence of living adult specimens of *Velutina velutina* in the Sound, it is probable that larvae of this species may occur in the plankton. And the large larva shows, indeed, features which are highly reminiscent of those presented by the *Velutina* larva figured by LEBOUR. The only difference is that LEBOUR'S larvae are colourless (with pale brown spots on the body, according to the coloured plates of LEBOUR), while in our larvae the velum has reddish-brown borders of pigment. As is known from *Aporrhais pes pelecani* (which see), such differences in the pigmentation may be due to local variations, and this is probably the case here.

Summarising the above considerations, I am of opinion that all the *Echinospira* larvae hitherto found in the Sound belong to *Velutina velutina*, differing from the Plymouth specimens in the pigmentation of the velum. Three of the larvae from the Sound are younger than anyone seen by LEBOUR and in this stage have a structure on the upper part of the *Echinospira* shell which agrees entirely with that on the larva referred by BERGH to *Onchidiopsis*. Probably BERGH was wrong in his conjecture, and his larvae may just as well belong to *Velutina* —or, if he is right, the youngest stages of these two genera are so similar that it will be impossible to separate them in the plankton. The larvae of *Capulus hungaricus* (see this species) may also be confused with those of *Velutina*, but as *Capulus* is extremely rare in the Sound, it seems justifiable to refer the larvae found to *Velutina*, which is of common occurrence.

Velutina plicatilis (O. F. MÜLLER) (= **V. flexilis** (MONT.)). Two specimens recorded from Hellebæk prior to 1880; not found later.

Reproduction: A. Literature. PELSENEER describes and figures (1906a) a Lamellariid larva from the Gulf of Biscay, and LEBOUR (1935b, p. 167) discusses this larva and states that "although this (the shell) is harder and more distinctly nautiloid than the present species (viz. *Velutina velutina*), yet it has somewhat the same form and may belong to the same genus". The *Echinospira* shell proper is rather cartilaginous, much compressed, nearly planorbiform, and the true shell has $2^1/_2$ whorls and a very large aperture. The velum has four long lobes, apparently without pigmentation; eyes and right tentacle were distinct. The identification of the larva, however, is dubious, and in 1937 LEBOUR states that "the larva of *Velutina plicatilis* is unknown".

B. Own remarks. Nothing is known about the reproduction from the Sound.

Trophon truncatus (STRØM). Northern part of the Sound, rather common locally.

Reproduction: A. Literature. The reproduction of this species is unknown. — The closely allied species *Trophon clathratus* (L.) var. *gunneri* LOVÉN, examined by THORSON (1940a), has lens-shaped egg capsules laid singly and attached to the substratum by a flat base. There is a preformed exit-hole at the top (covered by a thin membrane), whence two ridges issue, which divide the capsule into two nearly symmetrical halves. The development of this species is non-pelagic, the young hatching in the crawling stage. The lusitanian species *Trophon muricatus* (LEBOUR 1936, p. 560—61) has egg capsules of a similar type, but the individual capsule contains only a few large-sized eggs, 480 μ in diameter. The development is non-pelagic.

B. Own remarks. In the Little Belt off Røgle Klint, depth 40 m, *Modiola* epifauna, two egg capsules attached to stones were collected on $^{28}/_{7}$-44. The lens-shaped capsules with a preformed exit hole and two ridges to the margin bore a close similarity to those known from *T. clathratus,* and as similar egg capsules laid by Danish species of *Bela, Mangelia,* or *Philbertia* were well known beforehand or could be left out of account in the locality in question, the capsules could be referred without doubt to *Trophon truncatus,* which was present in adult living specimens in the same samples. A comparison of the largest embryos in the capsules with the apex (fig. 134 G) of the adult supplied the final proof. — One of the capsules found contained 11 rather young embryos (fig. 134 A), the other 6 large, clumsy young just ready to hatch (fig. 134 C) with the velum totally reduced and crawling lively about on the inner side of the capsule. On $^{31}/_{7}$-44 one more egg capsule was found at the same depth and in the same locality on an empty shell of *Modiola* (fig. 134 B) containing 9 embryos (fig. 134 D) which had just commenced to form the first cup-shaped shell.

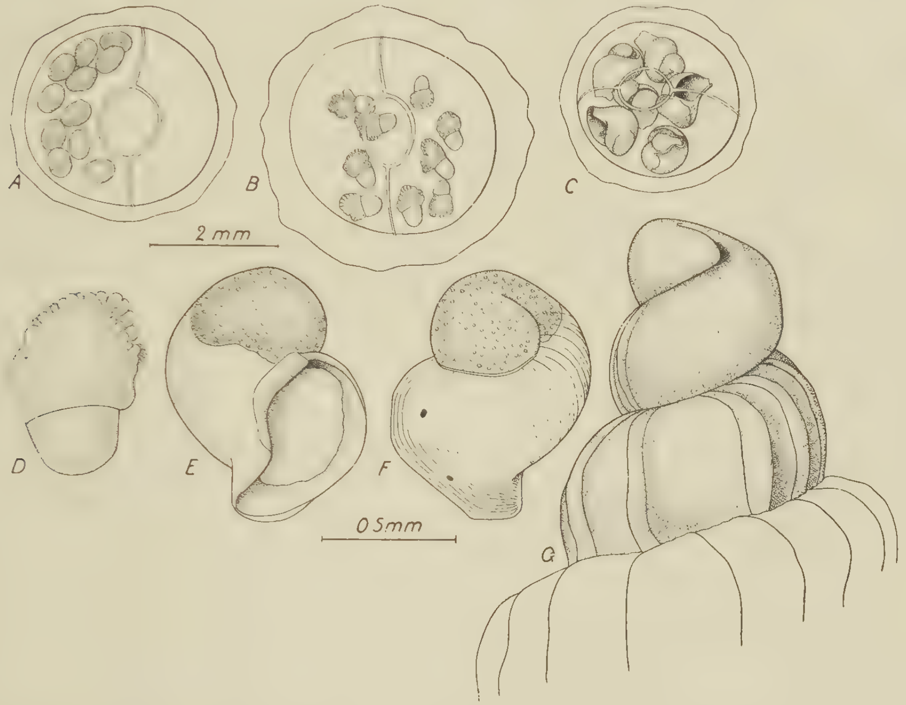


Fig. 134 A-G. *Trophon truncatus* (Strøm). Egg capsules and development. — *A* to *C.* Egg capsules taken off Røgle Klint in the Little Belt, depth 40 m, on stones and dead shells of *Modiola.* Drawn from life on the day of capture. — *A.* Capsule with 11 young embryos ($^{28}/_{7}$-1944). — *B.* Capsule with 9 embryos with cup-shaped shells ($^{31}/_{7}$-1944). — *C.* Capsule with 6 embryos ready to hatch ($^{28}/_{7}$-1944). — *D.* Embryo from the capsule fig. 134 B at larger magnification (drawn from life on $^{31}/_{7}$-1944). — *E* to *F.* Embryos nearly ready to hatch from the capsule fig. 134 C, drawn from life on $^{30}/_{7}$-1944. Seen from the ventral side (E) and from the dorsal side (F). — *G.* Apex of young bottom stage from the North Sea, depth 56 m, drawn from a specimen in the Copenhagen museum. (The 2 mm-scale refers to fig. A to C, the 0.5 mm-scale to figs. D to G).

The capsules, 1.3 to 2.1 mm across (1.8 to 3.1 mm across when the basal membrane is included), are smooth, transparent and colourless. — The embryo in the crawling stage (fig. 134 E—F) has a colourless, transparent, clumsy shell with a broad siphon, two black eyes situated at the base of a pair of large tentacles, a cream-coloured liver, and a group of whitish granules showing through the shell in the last whorl. The rest of the animal is greyish-colourless. No pelagic stage.

All species of *Trophon* from the North Atlantic hitherto examined have, thus, lenticular egg capsules and a non-pelagic development. *Trophon (Xymene) hanleyi*, described by Hedley (1917) from Australia, has similar egg capsules and — as seen from the figures — the eggs are about 500 μ across, indicating a non-pelagic development. — The egg capsules of *Trophon geversianus* described by Strebel (1905) and Melwill & Standen (1898—1900) from the Magellhaen Strait and the Falklands are so different from those of the other species known that *T. geversianus* should probably be referred to a new subgenus. The development of this species is likewise non-pelagic.

Nucella lapillus (Linné). One living adult specimen found on the Hittarp reef, northern part of the Sound, 16—20 m, red algae, *Laminaria*, on $^{7}/_{7}$-41.

Reproduction: A. Literature. Ankel (1936a, 1937, 1938b), Selenka (1872), Carpenter (1855, 1857 a and b), Portmann (1925, 1926, 1930b), Koren & Danielssen (1846, 1852, 1853, 1856, 1857), Lebour (1937a), and Pelseneer (1905, 1911) have studied and figured the egg capsules and the development of this species. The eggs are laid in vase-shaped capsules, arranged side by side in layers on stones or rocks. The yellowish-brown capsule is 7—9 mm high, and 2 mm across and "attached by a wide, flat base with a thin stalk supporting a narrow oval vase". Each capsule contains some hundred eggs (up to 1000), of which only 15—25 hatch out at Plymouth, and about 35 at Roscoff; the other eggs fall to pieces and form a column of yolk in the middle of the capsule on which the embryos feed. Such embryos, sucking on the stock of yolk, are quite sac-shaped; the organogenesis is stopped until all the yolk has been stored in their intestines. The larvae hatch in the crawling stage through the exit hole at the top. When hatching (cf. Ankel 1937, fig. 12), they have yellowish-white shells with nearly two whorls. Breeding all the year round. The development from fertilisation to hatching takes about four months.

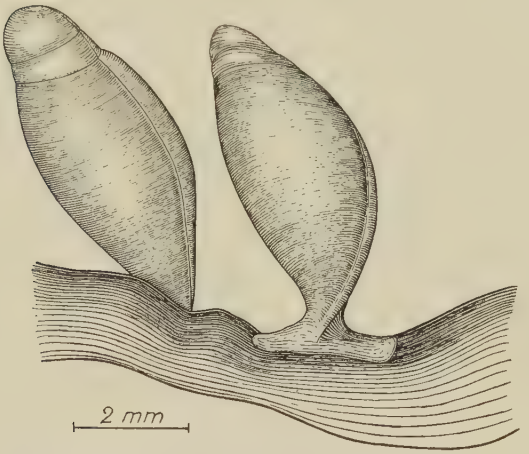


Fig. 135. *Nucella lapillus* (Linné). Egg capsules attached to a *Laminaria*-hapteron. Taken on the Hittarp reef, depth 10—12 m, on $^{9}/_{7}$-1941. Drawn from life on the same day.

B. Own remarks. On $^{9}/_{7}$-41 two egg capsules of this species were found attached to hapterons of *Laminaria* on the Hittarp reef, 10—12 m (fig. 135). One of the capsules was empty, but the other had a column of yolky grains, on which young, sac-shaped embryos were feeding. The mode of development is thus the same in the Sound as in all other localities where egg capsules of this species have been examined.

Sipho propinquus (Alder). Northern part of the Sound, rather rare.

Reproduction: A. Literature. Jeffreys (1867, p. 339) has described, but not figured, the egg capsule, which is hemispherical and margined by a narrow membrane and contains one embryo only. There is no preformed exit hole at the top. The egg capsules are laid singly.

B. Own remarks. A single egg capsule was taken west of Viken in the northern part of the Sound, depth ?, on $^{12}/_{6}$-39, by fil. dr. H. Brattström, Zoologiska Institutionen at Lund, and kindly placed at my disposal. This capsule (fig. 136) had a basal diameter of about 5 mm (6 mm when the basal membrane is included) and a height of $3^{1}/_{2}$—4 mm. The colour was yellowish-brown, but there was an oval area on one side of the capsule which differed somewhat in colour from the remaining part, viz. the exit hole. As in all species of *Sipho* hitherto examined the embryos feed on nurse eggs (each nurse egg measures about 110 μ across), and hatch in the crawling stage. The capsule contained, however, only quite young undeveloped eggs.

Neptunea antiqua (Linné). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. Baster (1762), Jeffreys (1867, with figs.), Meyer & Möbius (1872, with figs.), Dons (1913a, with figs.), and Thorson (1935a, figs., 1941b, figs., for the Arctic variety *despecta*) describe the spawn. Up to a hundred capsules are deposited in a cluster, which often has the shape of an irregular corn-cob. Each capsule contains several thousands of eggs, but only two to four of these develop into embryos, the others serving as food for these ("nurse eggs"). Each embryo seems on an average to feed on 2500 nurse eggs, and the young, which consequently leave the capsules in the crawling stage without any pelagic life, when hatching have a hardened calcareous shell of two whorls, 6—8 mm long. The exit hole is a wide slit situated near the margin at the distal end of the under side. Spawning at Plymouth during the latter part of the winter.

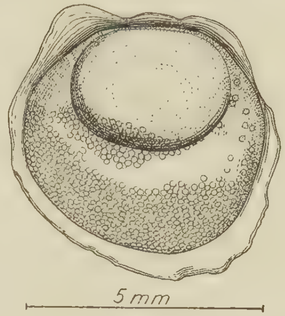


Fig. 136. *Sipho propinquus* (Alder). Capsule with newly laid eggs, seen from above. The oval membrane occupying nearly half of the dome-shaped upper capsule wall covers the exit hole. West of Viken (northern part of the Sound), depth?, on $^{12}/_{6}$-1939 (drawn from a specimen preserved in alcohol).

B. Own remarks. On April 2nd, 1942, two egg clusters were taken off Snekkersten at a depth of 20 m, both of them with embryos ready to hatch. The average number was two embryos per capsule. On $^{10}/_{7}$-42 another egg cluster was obtained off Hellebæk, at a depth of 25—30 m. It contained quite undeveloped eggs. As the embryos grow to such a considerable size within the egg mass, it seems reasonable to suppose that they will take at least two months from spawning to hatching (cf. the remarks of Portmann (1925, p. 528) on the slow development in *Buccinum*). This means that, judging from our few finds, the season in which egg capsules may be found in the Sound lasts from early February to the middle of September. Egg clusters of *Neptunea* from other Danish and adjacent seas kept in the Copenhagen museum were collected on the following dates: $^{10}/_{5}$-07 (Skagerrak, young in the crawling stage ready to hatch); $^{12}/_{6}$-33 (NNE. off the Skagen light-vessel, young embryos still without shells); $^{30}/_{7}$-44 (the Little Belt, 30 to 40 m depth, several egg masses with newly laid eggs as well as with medium-sized embryos); $^{28}/_{8}$-1900 (Great Belt, 20 m, young eggs and no visible embryos); $^{2}/_{9}$-34 (Kristineberg, Bohuslän, large embryos with shells), and $^{12}/_{10}$-06 (Læsö Rende, some capsules with medium-sized embryos, others empty with open exit holes). These dates compared with those from the Sound seem to indicate that spawning takes place at any rate from February to October (November). From the actual winter season only very little material is at hand, but it seems most likely that spawning specimens may be found throughout the year.

The egg mass from Skagerrak contained 1—2 large embryos per capsule measuring: 6.6 × 12.7 — 6.4 × 12.1 — 6.4 × 11.7 — 6.2 × 12.1 — 6.2 × 11.7 — 6.3 × 11.3 — 6.1 × 11.9, and 6.0 × 10.4 mm respectively. The diameter of the undeveloped egg is 300 μ, and capsules of the size found in the Skagerrak usually contain about 5000 nurse eggs each. The number of embryos found in five capsules from Læsø Rende were 1 — 1 — 1 — 1 and 2 embryos respectively. The observations seem to show that the embryos feed exclusively on nurse eggs, and that "cannibalism" – unlike the conditions in *Buccinum undatum* — does not take place. As smaller animals lay smaller capsules than the larger animals, and as the number of embryos per capsule may vary, the variations in the size of the hatching young may be very large.

Buccinum undatum Linné. Northern and middle parts of the Sound, common.

Reproduction: A. Literature. Figures and (or) descriptions of the spawn have been given i. a. by Dons (1913 a, b), P. Fischer (1887), Baster (1762), Jeffreys (1867), Koren & Danielssen (1846, 1852, 1853, 1856, 1857), Lebour (1937 a), Lubbock (1860), Möbius (1891), and Thorson (1941 b). — Portmann (1925, 1926, 1927, 1930 a) gives excellent observations on nurse egg feeding. — The egg capsules are laid in irregular clusters resembling large sponges. The largest number of capsules deposited in a cluster by a single female is about 2000, but often several specimens lay their egg capsules in a common cluster, which may contain a number of up to 15000 capsules (Dons 1913 a). Small adults (dwarf-forms) may produce smaller egg-capsules than large adults (Dons 1913 b). The single female may deposit several egg clusters at intervals of about five days (Baster, l. c.). Each capsule contains on an average 1000 eggs, but only c. 30 of these develop into embryos. The greater number of eggs will not develop at all and are gradually devoured by the embryos. The "nurse eggs" in *Buccinum*, however, will not fall to pieces as in *Nucella*, but are quite intact when eaten. The organogenesis in the embryos takes also place during the period of nurse egg feeding. When all the nurse eggs have been devoured, the embryos within the individual capsule will begin to eat each other ("cannibalism"), and only about ten embryos with a shell of $2^1/_2$ whorls and 1 mm in height will hatch from each capsule after having devoured their brothers and sisters. Each embryo has thus on an average had about 100 nurse eggs at its disposal. The embryos hatch in the crawling stage without any pelagic life. The largest number of hatching young from a single cluster laid by a single female may be estimated at 20,000. Lebour (l. c.) states that at Plymouth "the spawning season is between October and May according to locality". Havinga (1922, p. 388) mentions spawning at Holland (Zuidersee) in winter but not later than May. Sykes (1905, p. 75) has observed spawning at Ireland during October-November, "but live spawn masses are to be found from that period until August, when the young have been observed hatching". Aurivillius (1898 b) has found egg clusters with large embryos during the whole period from February to September near Kristineberg, i. e. breeding takes place nearly the whole year round.

B. Own remarks. Egg clusters from the Sound were collected on: $^6/_2$-43 (off Snekkersten, depth ?, 3 egg clusters with young eggs); $^1/_3$-43 (same locality, 2 egg masses both of them composed of a majority of capsules with quite young eggs and a smaller number of capsules from which the young had already emerged. Capsules with large embryos were, however, not found); $^{10}/_3$-43 (same locality, 3 egg clusters, all with newly spawned eggs); $^2/_4$-42 (same locality, depth 20 m, 1 large cluster with newly spawned eggs and with empty capsules from which the young were hatched through the open exit holes). Further, an egg cluster with young eggs is present from the Sound taken on $^9/_6$-37 (leg. H. Brattström, Zool. Inst., Lund) and the same scientist has handed over to me an egg cluster from Flinttrännan between the Kalkgrundet light-vessel and Malmö, taken on $^9/_7$-34, which contained embryos ready to hatch and several empty capsules. — Egg clusters from other parts of the Danish seas now found in the Copenhagen museum were taken on the following dates: $^7/_3$-03 (Skagerrak, 220 m, embryos hatched from most of the capsules, some capsules still with undeveloped nurse eggs); $^{13}/_3$-1906 (Pakhusbugten, Aarhus, numerous capsules with eggs just laid, other empty capsules with open exit holes from which the embryos had hatched; the cluster had been laid by several specimens); $^{18}/_{4}$-30 (Gåsö Ränna, empty capsules with embryos hatched); $^{22}/_{5}$-07 (4 miles E. of Nordre Ronner, N. Kattegat, embryos ready to hatch); $^{30}/_{7}$-44 (the Little Belt, 30 to 40 m depth, several egg masses with newly laid eggs as well as with hatching embryos), and $^{23}/_{8}$-33 (the North Sea, 55°58′ N. 5°57′ E., newly laid, undeveloped eggs). Prof. R. Spärck has informed me that on April 1st, 1943, when he examined several dredge hauls in the western Limfjord (N. Jutland), newly laid egg masses of *Buccinum undatum* occurred in large numbers. From the inner Danish waters egg capsules are thus present from the period $^{6}/_{2}$ –$^{30}/_{7}$. However, it may be supposed that the development within the egg capsule is rather long, at least 2 months, and accordingly the empty capsules from $^{13}/_{3}$ must have been spawned early in January. The find from the North Sea seems likewise to show that spawning takes place during the whole year, with a pronounced maximum in the late winter and spring.

Nassa reticulata Linné. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Jeffreys (1867), Meyer & Möbius (1872), Ussing (1932), and Ankel (1929) describe and figure the egg capsules. The latter author gives interesting data on the way in which they are laid. Pelseneer (1911) and Lebour (1931 c, 1937 a) describe and figure the capsules, the embryos, and the pelagic larvae. Their combined results may be summarised as follows: Breeding season near Kiel January to May, near Plymouth March to August, in the Channel from late April to late August. A few capsules are probably also laid outside these seasons. The egg capsules, 4.8—5 mm high, are horny, flattened and bottle-shaped, "the pouch is flattened in one direction and almost round in the other" and "fixed by a flat base, then narrowing and enlarging again into the vase". The capsules are deposited singly or — more commonly — in rows on *Zostera, Fucus,* stones, or shells. Each capsule contains 50—100 eggs, 160 μ across, all of which develop. When hatched, about one month after having been spawned, the smooth, unsculptured, very transparent shell, 280—300 μ across, with $1^{1}/_{2}$ whorls, has a very pronounced "beak" on the outer lip. The velum is bilobed with a reddish-brown border, four-lobed in older larvae. In the last period of the larval life the shell has three whorls, and is 720—800 μ across. The canal is formed, and tentacles are distinct. Brownish-black pigmentation on the foot. It is in this stage that the metamorphosis takes place.

B. Own remarks. Egg capsules (fig. 137 A—B) of this species have been observed in the Sound in the period from $^{20}/_{6}$ (1942, off Hellebæk, 15 m, numerous capsules all with newly spawned eggs) to $^{21}/_{8}$ (1936, off Ven, 15 m, 21 capsules with newly spawned eggs). The maximum occurrence of egg capsules seems to be July to August (e. g. $^{4}/_{7}$-42, Hellebæk-Julebæk, 8—12 m, large quantities of egg capsules, and $^{4}/_{8}$-41, off Julebæk, lots of capsules with eggs or embryos). The larvae from the Ven capsules taken on $^{21}/_{8}$ hatched about one month later, i. e. in the last days of September. — Six capsules examined on Ven on $^{8}/_{7}$-36 contained about 100 eggs each. Ten egg capsules with newly laid eggs examined at Hundested (the Isefjord) in July 1943 contained: 160 — 196 — 200 — 201 — 203 — 205 — 210 — 234 — 235, and 303 eggs respectively, i. e. an average of 215 eggs per capsule.

Larvae are almost absent or very rare in the plankton during the actual winter period. In April, in some years even later, the first larvae are seen in the plankton. The first observations in the Sound were made on $^{18}/_{4}$-37; $^{6}/_{6}$-38; $^{10}/_{4}$-39, and $^{10}/_{4}$-42. In April and May only a few larvae are present, and also in June and sometimes in the first part of July only a few larvae may be found. From the middle of July they increase considerably in number, attaining their maximum occurrence late in August and September, e. g. off Ven on $^{9}/_{10}$-37 (249 larvae per main series) and off Helsingør on $^{25}/_{7}$-42 (490 larvae) and $^{17}/_{9}$-41 (1460 larvae per main series), where they were among the dominant larvae in the plankton. In the course of October they decrease in number, and in November only a few larvae are found in each main series. Few and scattered larvae may occur in December, and occasional larvae even in January, February, and March. Larvae may thus be found all the year round, but they are rare in winter and absolutely dominant in August-September. As late as August many of the larvae are quite young and newly hatched, which is in good agreement with the capsules examined. — It would seem to me as if the first few larvae in the early spring originate from parents in the northernmost part of the Sound at depths of 1—2 m only. As soon as the surface water is heated by the sun, these specimens will begin to spawn. By far the greater number of the adult *Nassa* live at depths of from 6—15 m or more, where the heating of the water sets in somewhat later in the summer. The spawning will presumably reach its maximum in July and early August, and as the eggs and embryos will spend a month within the egg capsules before hatching, the larvae will reach the planktonic stages in August to September. Larvae found later in the year have probably been spawned by parents living in still deeper water (at depths up to 35 m), where the maximum temperature is reached in September, October and November.

The hatching larvae (fig. 137 C—F) found at Hundested were 265—295 μ across the shell, which had $1^{1}/_{4}$ whorl. The shell is quite colourless and structureless apart from a few lines of growth near the aperture, which has a very pronounced "beak". The bilobed (faintly four-lobed) velum has a reddish-brown pigmentation along its margin, brownish pigment is seen in front of the foot and bluish-black pigment in the hindmost part of the intestine. The liver is yellowish or yellowish-grey, the stomach grey. Two large statocysts, two black eyes. The somewhat older, pelagic larvae (fig. 137 G—H) from the Sound have a distinct keel on their shells, which at its terminal point forms the "beak" at the mouth.

The shell is now provided with minute dots arranged in spiral striae, and the canal is formed. The liver is greenish-grey, the velar pigment purplish-black, and large spots of yellow pigment (in direct light) is seen in the foot. The oldest stages of the larvae (fig. 137 I) have been described so well by LEBOUR (l. c.) that no new description seems necessary. They are easily recognisable by their quite transparent, colourless shells with the fairly much elevated spire and the olive-green-yellowish liver (the shell e. g. of *Rissoa inconspicua* is yellowish-horn-coloured and less elevated). — In the Isefjord several egg capsules with young eggs were seen on *Zostera* and *Fucus* on $^{5}/_{6}$-43, and in the same locality egg capsules with young eggs as well as embryos in all stages of development were abundant in July 1943.

Nassa pygmaea LAMARCK. Northern and middle parts of the Sound, rare.

Reproduction: A. Literature. KAREN VESTERGAARD (1935) describes and figures the egg capsules and larval stages of this species from Frederikshavn (N.W. Kattegat): Spawning in July. The singly laid egg capsules (not in rows as in *N. reticulata*) are $2^{1}/_{2}$ mm high and $1^{1}/_{2}$ mm broad, with a somewhat broader basal part of the capsule than in the closely related *Nassa incrassata* (see this species), the capsules of which are probably often confused with those of *N. pygmaea*. Each capsule contains 40—50 eggs. The hatching larva has a shell, 200 μ across, of hardly more than 1 whorl and a small process on the outer lip. The bilobed velum has a reddish-brown border of pigment along the margin of each of the rounded lobes. Eyes, statocysts, and mouth are distinct. Older larvae from plankton belonging almost certainly to this species have a shell, 1000 μ high, of 3 whorls and with a faint radial sculpture. The

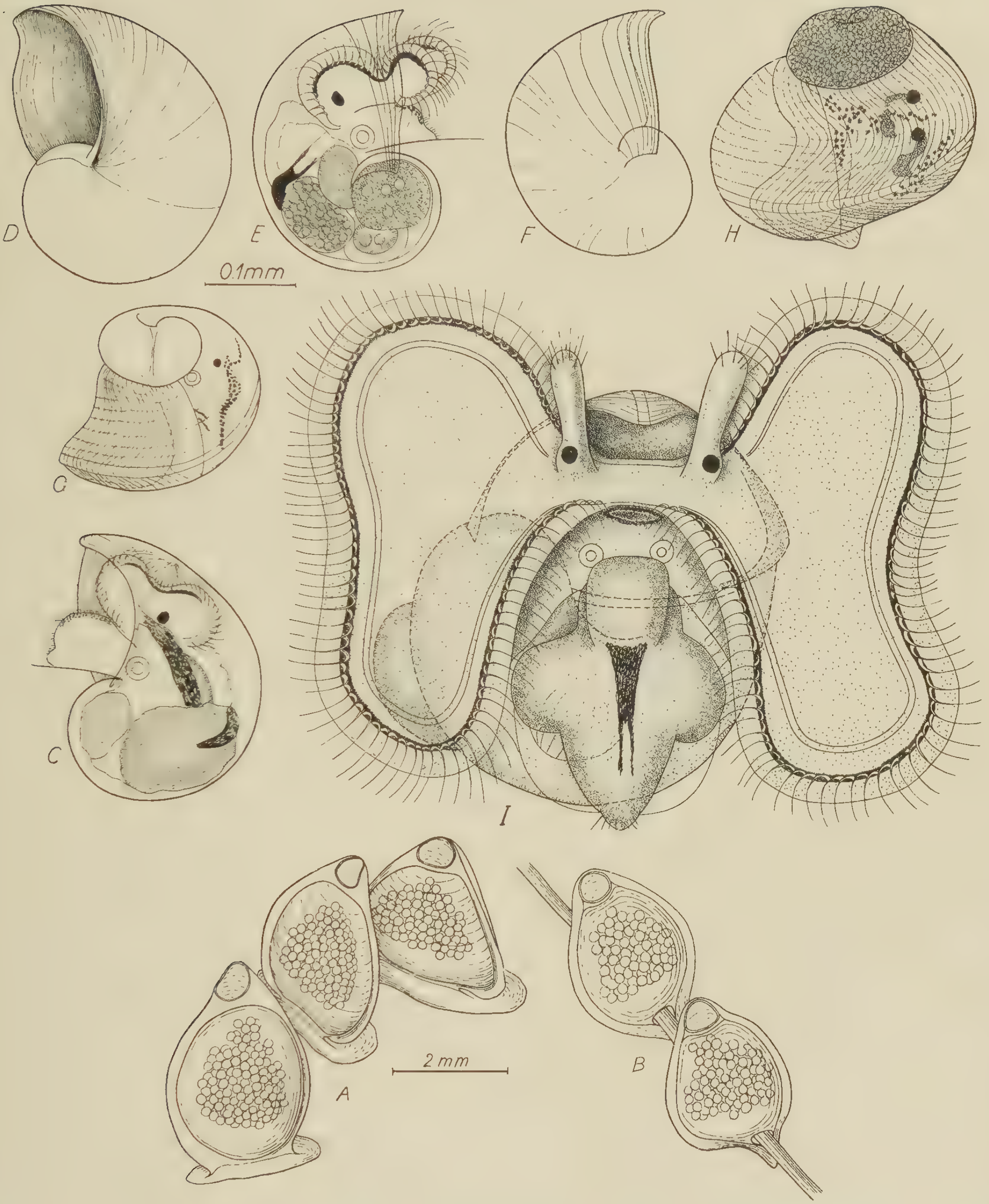


Fig. 137 A-I. *Nassa reticulata* LINNÉ. — *A*. Egg capsules attached to a piece of *Fucus*. Taken off Hellebæk, depth and date unknown. — *B*. Egg capsules attached to a red-algae stalk, off Ven, depth 10 m, caught and drawn from life on $^{8}/_{7}$-1936. — *C* to *F*. Young planktonic larvae just hatched from the egg capsules. Off Hundested (the Isefjord) in July 1943, drawn from life. Seen from the left side with the animal partly withdrawn (C); empty shell seen from the left side (D); shell with the animal partially withdrawn, seen from the right side (E); empty shell seen from the right side (F). — *G* to *H*. Young and medium-sized larvae, respectively, from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{4}/_{9}$-1937. The animals are withdrawn in their shells. Seen from the dorsal side. — *I*. Old larva swimming, seen from the ventral side. From plankton off Ven, depth 18-0 m, caught and drawn from life on $^{8}/_{8}$-1940.

outer lip has still a beak-like process. A four-lobed velum with a reddish-brown border of pigment; the velar lobes are rather long, but not so long as in *N. incrassata.* Two distinct tentacles, foot without pigment, with two "horns" in front.

B. Own remarks. Egg capsules of this species were found off the N.W. point of Ven, depth 14—16 m, on $^{12}/_{8}$-36 adhering to shells of *Aporrhais pes pelecani.* At Frederikshavn I happened to observe several egg masses of this species being laid in an aquarium on $^{20-25}/_{7}$-36 (fig. 138 A—B). A single female deposited 16 egg capsules in the course of 4—5 days. The average number of eggs for a large number of capsules was 45. A doubtless observation of larvae of this species was only made once in the Sound, viz. off Ven on $^{15}/_{7}$-39 (2 large and 1 medium-sized larvae). An old swimming Veliger larva (shell 650 μ across) was sketched from Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30—0 m, on $^{24}/_{8}$-1945, and is figured here (fig. 138 C). The yellowish horn-coloured shell is larger and more globular than that of *N. reticulata* in the same stage, the liver is yellowish-green, the columella is dark-brown, and in the oldest stages the canal was already distinct. Bluish-black pigment is seen round the mouth, along the margin of the propodium, and along the middle of the slender foot. The four-lobed velum has two thin lines of brownish-black pigment along the margin and — between them — dots of yellow pigment. The larva fig. 138 C was in the swimming-crawling stage, and when crawling the foot showed all the movements so characteristic of the genus *Nassa.* — Younger stages of these larvae may have been overlooked in our plankton series or may have been confused with and referred to the larvae of *Nassa reticulata.*

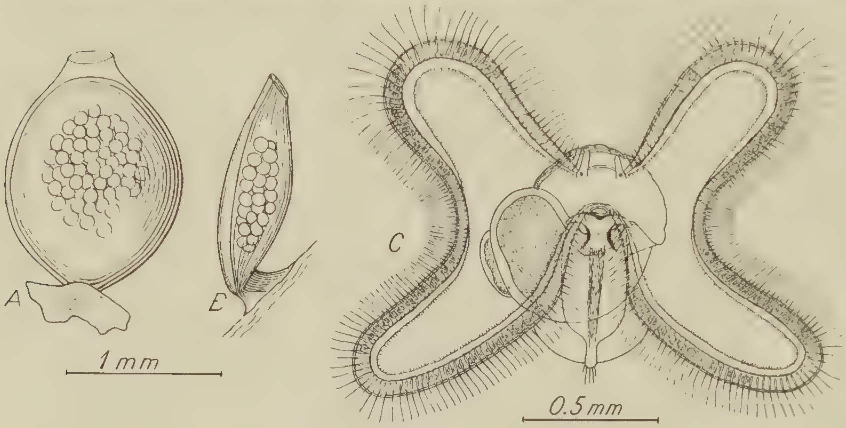


Fig. 138 A-C. *Nassa pygmaea* LAMARCK. Egg capsules spawned in aquarium on $^{22}/_{7}$-1936 by a female taken off Frederikshavn, NW. Kattegat (drawn from life the same day). — *A.* In front view. — *B.* In lateral view, attached to the substratum. — *C.* Old larva in swimming-crawling stage, here seen from the ventral side, swimming. From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30-0 m, caught and drawn from life on $^{24}/_{8}$-1945.

Nassa incrassata STRÖM. Northern part of the Sound, locally, e. g. on shelly banks in the Kattegat layer, not rare.

Reproduction: A. Literature. Egg capsules and larvae described by FISCHER (1892), and LEBOUR (1931 c, good figures, 1937 a) from Plymouth. Spawning nearly throughout the year, with a pronounced maximum in spring and summer. The egg capsules laid singly or in clusters measure 1.5—2 mm in height and are very similar to those of *N. pygmaea* (see this and fig. 138), but have a narrower base. Each capsule contains several eggs, 160 μ across, which all develop into embryos. The hatching larvae have shells, 180—200 μ across, with $1^1/_2$ whorls and a bilobed colourless velum. Older larvae have a four-lobed velum, which becomes very long in the latest stages. Each lobe has a brown spot of pigment at the end and a faint brown border of pigment along the margin. When the shell is 1500 μ high, the larvae leave the plankton and begin to crawl.

B. Own remarks. A few larvae belonging to this species were seen in plankton off Ven on $^{4}/_{7}$-39. They agree rather closely with the stage figured by Lebour (1931 c, pl. 4, figs. 5–6) and have thus only reached the intermediate stage of their planktonic development. The brownish-black spots of pigment were distinct on each velar lobe, and so was the marginal border of the same colour. The liver was olive-green; stomach, heart, statocysts, the large tentacles, and the two black eyes were distinctly seen. The shells measured 460—540 μ across. Plankton taken off Helsingør by the middle of July 1942 contained a single, fairly old larva of this species very like that figured by Lebour (1931 c, pl. 4, fig. 7) swimming readily about with four large velar lobes on which were distinct spots of pigment. These are the only observations available from the Sound, and the larvae in older stages have hardly been overlooked in our samples. — On $^{24}/_{8}$-1945 an old swimming larva (fig. 139) from Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30—0 m, was drawn from life. The shell was 760 μ across, and the velar lobes, which may be stretched out to twice the size shown in fig. 139, have large dark-purplish spots of pigment on the corners. A faint purplish-brown pigmentation is seen round the mouth, on the prostomium, and along the middle part of the foot.

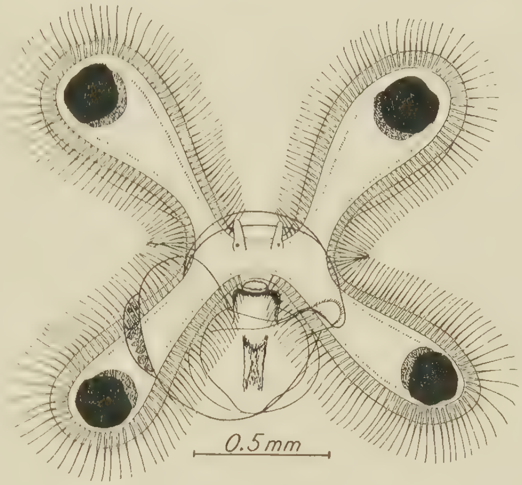


Fig. 139. *Nassa incrassata* Strøm. Old larva, swimming, seen from the ventral side. From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30-0 m, caught and drawn from life on $^{24}/_{8}$-1945.

Bela trevelyana Turton. Northern and middle parts of the Sound, rather common at fairly great depths.

Reproduction: A. Literature. The egg capsules and larvae of the present species are unknown. — Karen Vestergaard (1935) and Thorson (1935 a), however, have described the egg capsules of six different species of *Bela*, which all agree in the shape of the egg capsules, the characteristics of which are: Lens-shaped or slightly dome-shaped, with a narrow brim, solitary, and attached by the whole of their flattened base to a substratum. The exit hole is at the top, it is regular, oval, surrounded by a thickened edge, from which issue two ridges to the margin, dividing the surface into halves. This type of capsule, hitherto known for all species of *Bela* examined (and for *Trophon*, *Philbertia*, and *Mangelia*, which see) may be expected to be found in *Bela trevelyana* also.

B. Own remarks. Egg capsules of this type were taken off Ven on: $^{9}/_{7}$-36 (off Kyrkbacken, 19 m, on stones, 2 capsules, one of them empty, the other with about 25 young embryos); $^{10}/_{8}$-36 (N.W. of Ven, 14—17 m, on stones, 1 egg capsule with 31 embryos of medium size), and off Helsingør on: $^{7}/_{4}$-42 (off Hellebæk, depth 30 m, 1 capsule with dead embryos), and $^{20}/_{6}$-42 (off Hellebæk, depth 15 m, on shells of *Macoma calcaria*, 1 egg capsule with 31 embryos in the first cleaving-stages). In all these localities adults of *Bela trevelyana* were abundant, and as, moreover, the small number of embryos per capsule, viz. 25, 31, and 31, and the large size of the individual embryo and its type show that the capsules cannot belong to the other species of *Bela* occurring in the Sound, viz. *Bela turricola* (which see), or to *Trophon, Mangelia,* or *Philbertia,* the development of which is well known, it may be taken for granted that the capsules belong to *Bela trevelyana.*

The capsules (fig. 140 A—B) are 3.1 to 3.3 mm across and are so similar to those of other species of *Bela* that, if empty, they may hardly be identified with certainty. Unfortunately, no capsules within the material examined contained embryos ready to hatch. Only young eggs and larvae with the first small indications of a shell and with black eyes were seen. The oldest embryos found measured 300—350 μ in largest diameter, i. e. they were rather large, and besides they had a distinct violet tinge.

Large larvae which were present in plankton from the Sound, were followed until metamorphosis. The shell of the metamorphosing stages (fig. 140 H) showed such a close similarity to the apex of young bottom stages of *Bela trevelyana* (fig. 140 I—K) that the identification was easy and definite. The larvae (fig. 140 C—G) in the plankton are always very large and seem to hatch in this large size in a very late stage of development. The youngest planktonic larval shells found measured 355 μ across, i. e. almost the largest diameter of the largest embryos found. The oldest planktonic larva found (fig. 140 E—G) had a height of the shell of 710 μ and a breadth of 550 μ. The larval shell had 2 very broad whorls in the youngest stages found (fig. 140 C), and $2^1/_2$ whorls just before metamorphosis. The shell is rather globular, quite colourless, transparent, with a rather coarse structure consisting of spiral lines, which are connected with radial lines on the first whorl and with small dots on the top. The first whorl of the larval shell thus bears a rather great resemblance to the larval shells of *Alvania* and *Rissoa sarsi* (see these species), but is much larger and coarser. The larva has a very characteristic thick velum of a jelly-like consistency (fig. 140 E—G); it is bilobed, and each of the very large lobes is rounded and has a double border of violet pigment. The whole surface of the velum is provided with rather coarse verruciform tubercles. The liver is yellowish-brown, the body of the larva is yellowish-white (in direct light), and the pharynx has a faint purplish-red pigmentation. Two black eyes, and two large tentacles. Along the middle of the foot is a purplish-red stripe of pigment. Larvae in the stages shown in fig. 140 E—G were ready to metamorphose, and, while under observation, cast off all the cilia of the velum. The pelagic life of this larva seems thus to be very short. — A plankton haul, taken off Ven on $^{30}/_{7}$-40, depth 18—0 m, contained two large larvae and a young bottom stage, which had lost its velum and was able to crawl about (fig. 140 H). The final structure of the shell had appeared and proved to agree in all details with the apex of *Bela trevelyana* (fig. 140 I—K). The gills, the yellowish-brown liver, the bluish-black sections of the digestive system, and a large operculum were seen. Also the heart was distinct.

Larvae of this species were taken off Ven on: $^{6}/_{6}$-37 (6 spms.); $^{12\text{-}13}/_{8}$-38 (a few spms.); $^{4\text{-}5}/_{6}$-39 (4 spms.); $^{30}/_{7}$-40 (2 large larvae and 1 young bottom stage), and off Helsingør on: $^{27}/_{4}$-42 (2 spms.); $^{15}/_{5}$-42 (2 spms.), and $^{25}/_{7}$-42 (1 spm.). The main season is the actual summer time, but the occurrence of larvae in April as well as August seems to indicate that these larvae depend only to a rather small extent on the food conditions in the phytoplankton, a fact which is in good agreement with the short planktonic life of the larvae.

Bela turricola (MONT.). Northern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. Egg capsules and larvae described and figured by KAREN VESTERGAARD (1935) from Frederikshavn (N.W. Kattegat). The capsules, adhering to the shell of a living *Aporrhais,* were $2^1/_2$ mm across, and the shape was precisely the same

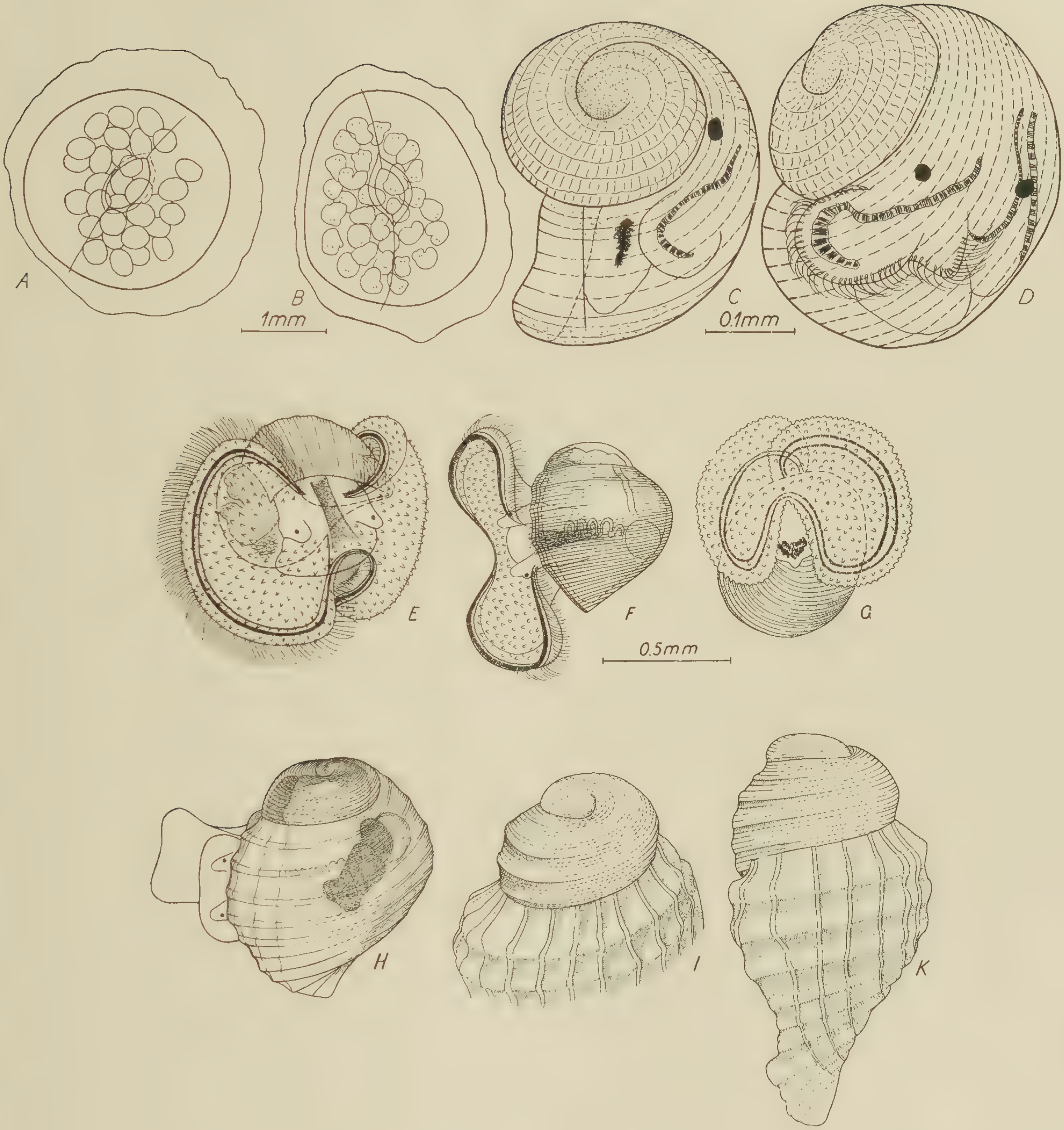


Fig. 140 A-K. *Bela trevelyana* Turton. · Egg masses and development. — *A*. Capsule with young embryos on shell of *Macoma calcarea*. Taken off Hellebæk, depth 15 m, on $^{20}/_{6}$-1942 (drawn dead). — *B*. Capsule with older embryos with distinct eyes. Taken off Ven, depth 14-17 m, on $^{10}/_{8}$-1936 (drawn from dead specimens in incipient dissolution on $^{19}/_{8}$-1936). — *C* and *D*. Young to medium-sized larvae in different views, taken off Ven, depth 18-0 m, caught and drawn from life on $^{5}/_{6}$-1939. — *E* to *G*. Old larvae from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{6}/_{6}$-1937 (G) and $^{30}/_{7}$-1940 (E and F), seen from the ventro-lateral side, swimming (E), the dorsal side (F), and the ventral side (G) — *H*. Young stage just after metamorphosis, crawling on the object glass and seen from the dorsal side. From plankton off Ven, depth 18-0 m, caught and drawn from life on $^{30}/_{7}$-1940. — *I* and *K*. Apex of young bottom stage taken off Hellebæk, depth 27 m (drawn from a dead shell in the Copenhagen museum).

as is described above for *Bela trevelyana* (see this species) and for the East Greenlandic species of *Bela*. Each capsule contains 100—150 eggs or larvae, which all develop and hatch when the longest diameter of the shell is 200 μ, and with hardly one whorl. The bilobed, rounded velum had large lemon-coloured spots of pigment along the margin and a very long foot bordered by reddish pigment. A right tentacle, eyes, statocysts and mouth were distinct. Later stages not seen.

B. Own remarks. The very characteristic larva has never been observed in our plankton, nor have the egg capsules been seen in the Sound.

Philbertia linearis (Montagu) (= **Clathurella linearis**). A dead, but fresh-looking, specimen was taken off Knähaken, 25—35 m depth, in the summer of 1942.

Reproduction: A. Literature. Jeffreys (1867) describes and figures egg capsules and newly hatched young, but according to Lebour (1934b, 1937a), who has thoroughly studied the reproduction of this species, the capsules and larvae of Jeffreys seem to belong to a different species. The egg capsules were laid in aquaria in February and March (at Plymouth), and larvae were found in plankton in spring and summer, rarely in the autumn. The singly laid capsules, 1500—2000 μ across, are of quite the same shape as those of the genus *Bela*, but according to Lebour (l. c.) have no ridges. They contain 60—80 eggs, each egg being 140—150 μ across (those referred by Jeffreys to this species contained 200—300 eggs). The larvae did not hatch out. Later larvae were, however, found in the plankton and were observed during metamorphosis. The larvae have dark, reticulated, very characteristic shells, a colourless velum, at first bilobed, later with four round, short lobes. The youngest larva seen was 196 μ across and had one and a half whorls, and a somewhat produced outer lip. In the late larva the shell is 800 μ long with four whorls.

B. Own remarks. The egg capsules were examined at Frederikshavn (N.W. Kattegat) on $^3/_7$-37. They were taken at a depth of 26 m attached to a stone. The individual capsule (fig. 141 A—B) agrees with the description given by Lebour (l. c.), who, however, failed to observe the two radial ridges. In an empty state these capsules are therefore hardly distinguishable from those of the genera *Bela* and *Trophon*. The large capsule (fig. 141 B) contained 114 embryos nearly ready to hatch, and the structure of the embryos provided a sufficient basis for a safe identification. The number of embryos in this capsule by far exceeded that stated by Lebour (60—80 eggs), and makes it probable that the capsules may vary very much as to size and number of eggs. Accordingly it is quite possible that also the capsules mentioned by Jeffreys (l. c.) belonged to the species in question. — On the same stone from Frederikshavn were five more egg capsules with undeveloped eggs. The type of capsule and the size of the eggs (150 μ across) were precisely the same, but the capsules contained only 51 — 55 — 55 — 59 and 62 eggs respectively. As these numbers agree fairly well with the egg number given by Lebour, it seems most reasonable to refer them to the same species. The hatching larvae (fig. 141 C) have dark purplish shells (240 μ across) with a characteristic "fenestrate" structure. The animal itself is colourless, it has a very long foot with long hairs at the end, and two black eyes. — The older larva (fig. 141 D) was only met with once in plankton from the Sound, viz. off Ven on $^{29}/_9$-36, and agrees entirely with the stages described by Lebour. Similar larvae were seen in plankton at Frederikshavn in July 1936 and July 1946.—In the last half of August 1945 larvae of this species were rather common in plankton from the Gullmarfjord (Bohuslän, Swedish W. coast), depth 40—0 m, and here I availed myself of the opportunity to make a detailed sketch of an old, swimming larva (fig. 141 E). The small operculum is hidden behind the foot of the swimming larva, and the four-lobed velum is rather small and quite colourless.

Mangelia brachystoma (PHILIPPI). Northern part of the Sound, rare.

Reproduction: A. Literature. The only species of *Mangelia* the egg capsules and larvae of which have been described and figured, is *Mangelia nebula* (MONTAGU) (cf. LEBOUR 1934b, 1937a). The egg capsules of this species, 1600 μ across, are lens-shaped, smooth, and transparent like those of *Bela* and *Philbertia*. No ridges were seen, but they may have been overlooked. Each capsule with about 60 eggs, 160 μ across. The hatching larvae have smooth shells, 230 μ across, and a bilobed velum (very large in older larvae) with conspicuous orange spots distributed over the lobes. Older larvae have shells with $3^1/_2$ to 4 whorls, 960—1000 μ long, the last whorl with tubercles. "The base (of the foot) is a pale grey, otherwise the animal is colourless". Breeding in summer.

B. Own remarks. The apex of a bottom stage of *M. brachystoma* is sketched in fig. 142 D.—The larvae of *Mangelia nebula* like those of *Bela turricola* are easily recognisable by their orange- or lemon-coloured spots of pigment on the velum. Larvae of these types have only been seen once in the Sound; they belonged, however, to the following species:

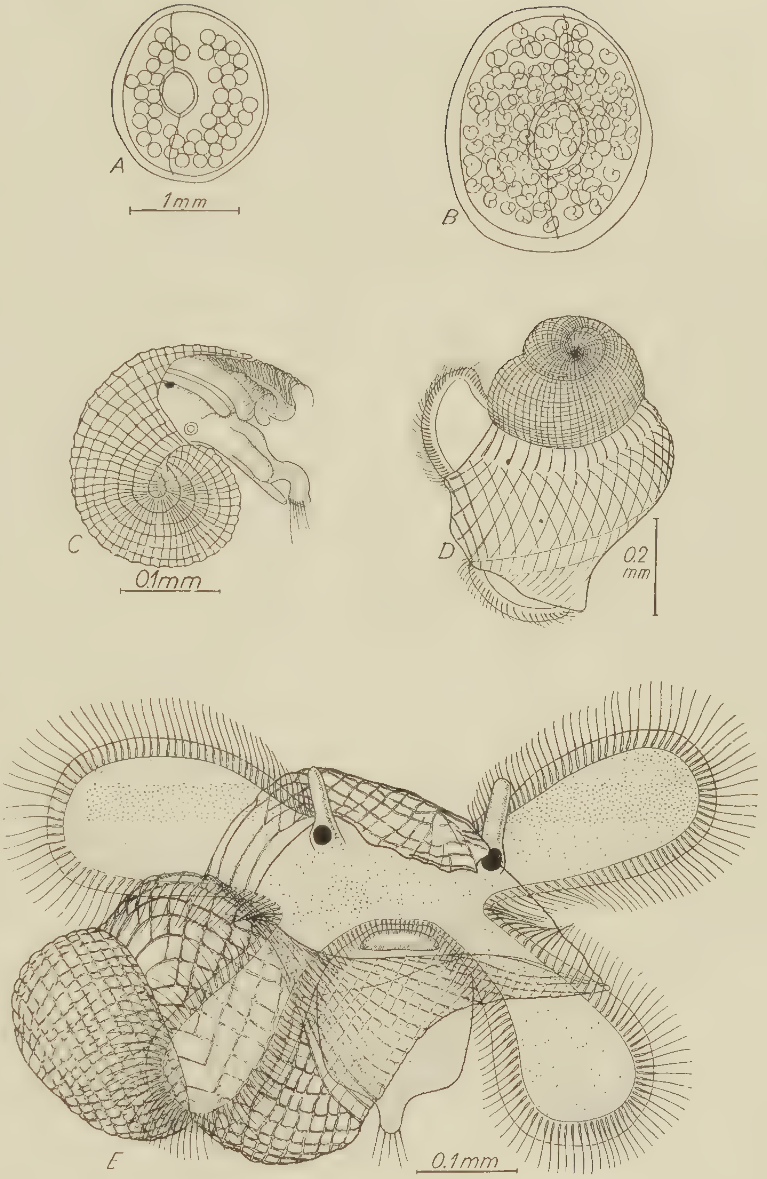
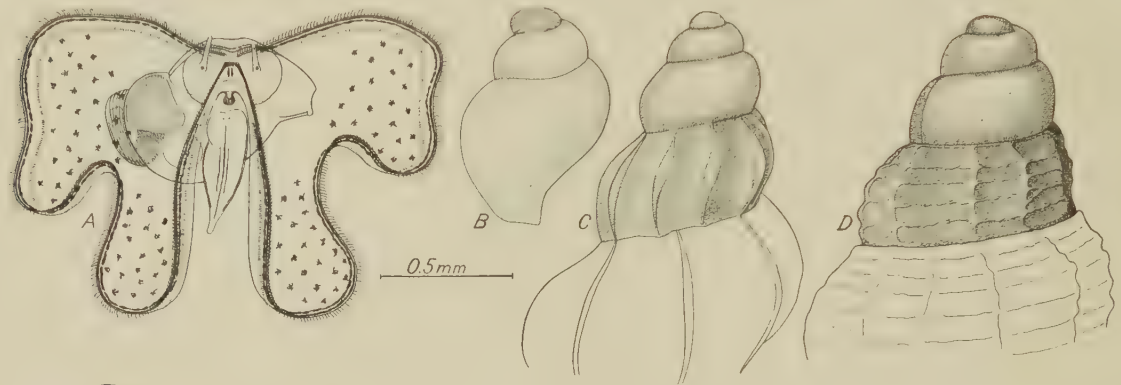


Fig. 141 A-E. *Philbertia* (*Clathurella*) *linearis* (MTG.). — *A* and *B*. Egg capsules taken off Frederikshavn (NW. Kattegat), depth 27 m, on $^{2}/_{7}$-1937 (drawn from life on $^{3}/_{7}$), substratum: stones. — *A*. Small capsule with young embryos. — *B*. Larger capsule with embryos nearly ready to hatch. — *C*. Larva hatched from the egg capsule fig. 141 B on $^{6}/_{7}$-1937 (drawn from life the same day). Shell dark purplish with coarse reticulations. Animal transparent, colourless; foot slender with long cilia. Seen from the right side. — *D*. Old larva from plankton off Ven, depth 20-0 m, caught and drawn from life on $^{29}/_{9}$-1936 (rough sketch by mag. sc. Erik Smidt). — *E*. Old larva, swimming, seen from the ventral side. From plankton off Kristineberg (Bohuslän, Swedish W. coast), depth 40-0 m, caught and drawn from life on $^{22}/_{8}$-1945.

Mangelia attenuata (Montagu). Two dead specimens are recorded from Hellebæk. Dead shells taken in recent years in the northernmost part of the Sound look rather fresh.

Reproduction: A. Literature. Unknown.

B. Own remarks. On $^{18}/_{8}$-44 occurred in the plankton off Ven, depth 18 to 0 m, a single very large larva (fig. 142 A), which swam actively about in the glass dish for several hours. The larva in question showed such a close resemblance to those of *Mangelia nebula* and *Mangelia ?coarctata* described by Lebour (1934 c, 1936 respectively) that the reference of our larva to this genus at once seemed quite certain. Our larva, however, deviated from that of *Mangelia nebula* in having a spirally striated apex like that of *Mangelia ?coarctata* from which it differed in having orange spots of pigment not only along the border of the velum but also over a large area of the velar surface, and in having purplish pigment on the foot.



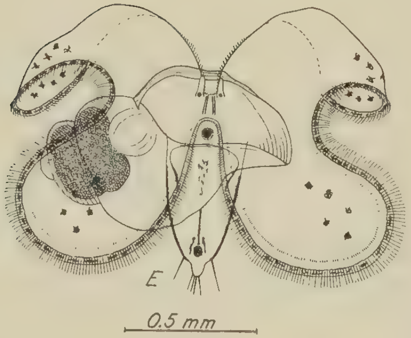


Fig. 142 A and B. — Old larva presumably belonging to *Mangelia attenuata* (Montagu) (See the text pp. 238–239). From plankton off Ven, depth 18-0 m, on $^{18}/_{8}$-1944 (drawn from life the same day). — *A*. Old larva, swimming, seen from the ventral side. — *B*. Larval shell of the same specimen seen from the dorsal side. — *C*. Apex (slightly worn) of adult *Mangelia attenuata* taken off Frederikshavn (NW. Kattegat), depth 27 m, on $^{30}/_{7}$-1936. — *D*. Apex (slightly worn) of adult *Mangelia brachystoma* (Philippi) from the same locality and date as fig. C. — *E*. Old larva presumably belonging to *M. attenuata*. From Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30-0 m, caught and drawn from life on $^{9}/_{9}$-1945.

Three adult species of *Mangelia* may come into consideration in the Sound, viz. *Mangelia brachystoma* (rare in the Sound, but rather common in the northern and middle parts of Kattegat), *Mangelia coarctata* (a single specimen only known from the Sound, rather rare in the Kattegat) and *Mangelia attenuata* (dead, but fresh-looking shells in the Sound, common in the northern and middle Kattegat). The scarcity of *M. coarctata* in our seas as well as Lebour's description of a larva probably belonging to this species and differing from our larva seems to refer the latter either to *M. attenuata* or to *M. brachystoma*. As the larva found is an old specimen, taken in a plankton series which was teeming with Kattegat larvae, and in a season in which the south-going Kattegat current was extremely strong, it seems just as reasonable to refer the larva to *M. attenuata* as to *M. brachystoma*. A comparison between the larval shell (fig. 142 B) and the apices (fig. 142 C –D) of these two adult species pointed to *M. attenuata* as the parent, the apex of this species like the shell of the larva being more slender than those of *M. brachystoma*. The spiral striation, however, could not be seen in the adults, and is probably soon worn off in the bottom stage. Thus, it seems most reasonable that the larva in question belongs to *Mangelia attenuata*.

The larva fig. 142 A is probably near the stage of metamorphosis. It has a colourless, transparent shell, 940 μ long, with $2^3/_4$ to 3 whorls, a distinct siphon and fine spiral striae on the top-whorl. The four-lobed velum is very large and, when distended, completely covers the shell. The velum has short cilia along the margin, a brim of dark purplish pigment at the base of the cilia, and inside this a parallel brim of lemon-coloured pigment (in direct light). The majority of the velar surface has large orange spots. Purplish pigment is seen below the mouth and in lines along the middle and the margin of the slender, planarian-like foot. Heart and subvelum are distinct, the liver is yellowish-green. Two large tentacles, two black eyes. — A swimming larva in the same stage of development but seen in a somewhat different aspect was found and sketched (fig. 142 E) in Gullmarfjord plankton (Bohuslän, Swedish W. coast), depth 30—0 m, on $^9/_9$-1945. *Mangelia attenuata* was here the dominant species of *Mangelia* in the adult stage.

The larva was only taken once in a single specimen in our samples from the Sound.

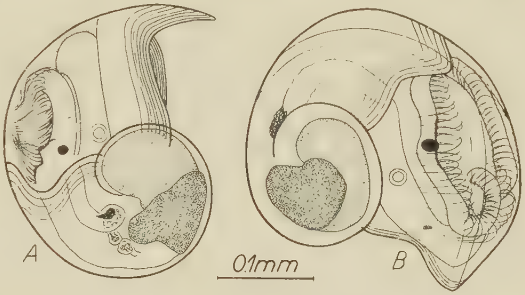


Fig. 143 A-B. — Prosobranch-larvae the identity of which is unknown (Prosobranch larva A, see the text pp. 239–240). From plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, caught and drawn from life on $^4/_8$-1942. — *A.* Young larva, seen from the right side. *B.* Older larva, seen from the dorso-lateral side. The shell is dark yellowish-brown, intransparent.

Mangelia coarctata (Forbes) (= **M. costata** Donovan). Some few living specimens known from Hellebæk.

Reproduction: A. Literature. Lebour (1936) describes and figures from Plymouth plankton a larva which she refers to this species, though the definite proof of its identity is not given. The larva in question has a "shell 1.25 mm high, first whorl and a half to two spirally striated, the last with longitudinal ribs and spiral lines giving it a somewhat reticulated appearance. Shell siphon fairly long, shell pale yellowish; foot pointed, animal siphon projecting from shell; tentacles rather long; velum very large, when in action almost covering the shell, four-lobed with large brown and orange spots round the border; animal greyish".

B. Own remarks. This larva is unknown from the Sound. See, however, the discussion under *Mangelia attenuata*.

Prosobranch larva A (fig. 143 A—B). Shell of young larvae 300 μ across, with $1^1/_4$—$1^1/_2$ whorls, rather thick-walled, yellowish-brown, opaque. The whorls with two distinct keels along their periphery, ending in the pronounced "beak" with several lines of growth, which forms a most characteristic feature of the outer lip. Distinct traces of an earlier "beak" with similar coarse lines of growth are seen on the last whorl even in the youngest planktonic stages met with. Along its outer margin the bilobed velum has a rather thin but distinct border of black pigment. Bluish-black pigment is seen in the middle part of the intestine. The right liver lobe is brownish-black, the left one yellowish-brown with fine granulations. A sub-velum, a ciliated foot, operculum, two small statocysts, and two black eyes are seen. The oldest larvae found, 350 μ across their shells, have very narrowly twined whorls and a deep dark brown colour of the shell.

In the main series taken off Ven these larvae were not counted separately, but together with other unidentified larval Prosobranchs. Off Helsingor they were present on: $^{19}/_{12}$-41 (2 larvae); $^{4}/_{6}$-42 (99 larvae in all stages of development, small larvae in the majority); $^{20}/_{6}$-42 (17 medium-sized and large larvae); $^{6}/_{7}$-42 (7 medium-sized larvae); $^{18}/_{7}$-42 (26 larvae in all stages), and $^{17}/_{8}$-42 (two medium-sized larvae). The main season of occurrence is accordingly June to July, which seems to show that the larvae originate from parents living at smaller or intermediate depths in the Sound. The majority of small larvae seem further to show that they mainly originate from parents living in the Sound or the adjacent waters. Most probably these larvae may be referred to one of the species of *Rissoa* found in the Sound the reproduction and larvae of which are still unknown.

General Discussion of the Prosobranchs.

At present the bottom stages of 64 species of *Prosobranchia* are known from the Sound. To these may be added five further species, viz. *Alvania punctura, Coecum glabrum, Odostomia conoidea, Philbertia linearis,* and *Mangelia attenuata* which are known from the Sound in such old larval stages that they may be supposed to metamorphose and settle there. Thus, so far the fauna of the Sound comprises a total of 69 species. — For 61 out of these 69 species — i. e. $88^1/_2$ per cent — the larval development is known in more or less rough features but sufficiently well to indicate the "ecological type" to which each larval species should be referred. These 61 species may be classified as follows (for species marked with an asterisk new data or a discussion on the reproduction or the larval occurrence in the Danish waters are given in the special part of this paper):

A. Viviparous Species: 2 = 3.25 per cent, viz. **Littorina saxatilis* and **Hydrobia jenkinsi* (both with non-pelagic larvae).

B. Species with a non-pelagic development: 19 = 31.25 per cent, viz. *Gibbula tumida*, **Neritina fluviatilis* (nurse eggs); **Lacuna pallidula*; **Littorina obtusata*; **Onoba striata*; **Hydrobia ventrosa*; *Liostomia clavula* (judging from the apex); **Brachystomia rissoides*; *Evalea insculpta* (judging from the apex); *Parthenina interstincta* (judging from the apex); *Parthenina indistincta* (judging from the apex); *Partidula spiralis* (judging from the apex); *Amauropsis islandica*; **Lunatia pallida*; **Trophon truncatus*; **Nucella lapillus* (nurse eggs); **Sipho propinquus* (nurse eggs); **Neptunea antiqua* (nurse eggs), and **Buccinum undatum* (nurse eggs).

C. Species with a very short pelagic life (often only a few hours to a few days): 5 = 8.25 per cent, viz. **Acmaea testudinalis*; ?*Acmaea virginea*; **Helcion pellucidum*; **Hydrobia ulvae*, and **Turritella communis*.

D. Species with a long pelagic planktotrophic larval life (cf. pp. 432—435): 35 = 57.25 per cent, viz. *Gibbula cineraria*; **Lacuna divaricata*; **Littorina littorea*; **Onoba vitrea*; **Alvania punctura*; **A. abyssicola*; **Rissoa sarsi*; **R. inconspicua*; *R. membranacea*; **Coecum glabrum*; **Bittium reticulatum*; **Triphora perversa*; *Scala clathrus*; **Aclis minor*; **Eulima distorta*; **Pelseneeria stylifera*; **Odostomia conoidea*; **O. acuta*; **O. turrita*; **Pyrgiscus rufus*; **Eulimella acicula*; **E. nitidissima*; **Capulus hungaricus*; **Aporrhais pes pelecani*; **Lunatia nitida*; **L. montagui*; **Velutina velutina*; **Nassa reticulata*; **N. pygmaea*; **N. incrassata*; **Bela trevelyana* (probably somewhat shortened pelagic life); *Bela turricola*, **Philbertia linearis*; ?*Mangelia coarctata*, and **Mangelia attenuata*.

Thus, 35 species out of the 61 species examined — i. e. nearly 60 per cent — have a long pelagic larval life, and it seems reasonable to assume, judging from the genera to which they belong, that these figures will not be essentially altered by the species whose mode of reproduction has not yet been examined.

The adult Prosobranchs constitute no large percentage of the bottom fauna in the Sound. In 300 bottom samples (PETERSEN 1911, table VI, no. III—VIII) taken all over the Sound the number of adult Prosobranchs which have pelagic larvae seems to constitute 4 per cent of the number of adult invertebrate specimens with a pelagic development on the level bottom, and a rough calculation indicates that they constitute about 10 per cent if the epifauna is also included. — The occurrence of Prosobranch larvae in the main series from the Sound agrees fairly well with this estimate, the larvae constituting 12.5 per cent of all the bottom animal larvae found in the plankton, viz. off Ven 14.7 per cent (45 main series) and off Helsingør 9.9 per cent (20 main series).

Fig. 193, p. 374, and fig. 194, p. 377, show the occurrence of Prosobranch larvae in our main series taken off Ven and off Helsingør respectively. The table on p. 372 is a supplement to the figures from Ven and comprises the main series taken in the period from August 1936 to August 1937, from which only an estimate, but no exact counts of the number of larvae, is at hand. — Off Ven (fig. 193) only one constant maximum a year occurs — in June to July — with larvae of *Littorina littorea* as absolutely dominant. This maximum decreases gradually during August-September-October, in the last two months with *Nassa reticulata* as the dominant larva; from December to April-May larval Prosobranchs are of little importance in the plankton. — The graphs from Helsingør (fig. 194) show quite similar results. Here, also, a *Littorina* maximum sets in in July, followed by a decrease in the number of Prosobranch larvae, those of *Nassa reticulata* being now most frequent until the winter minimum, from December to April, sets in.

Features common to the whole Sound are, then: From a pronounced minimum in December to March the larval Prosobranchs increase slowly in number in the plankton during the month of April. The larvae of *Aporrhais pes pelecani* and *Nassa reticulata*, which have a very long season of occurrence, are among the first forms to appear in scattered specimens, followed closely by the two typical spring larvae, *Lacuna divaricata* and *Rissoa sarsi*, both of which occur as early as April. In May the first few egg capsules and young larvae of *Littorina littorea* are seen, but the large swarms of *Littorina* larvae appear in June to July succeeded by smaller numbers of larvae of *Bittium reticulatum* — these two species constituting by far the majority of the "summer larvae" in the Sound. During August the *Littorina* larvae decrease gradually in number, to be replaced mainly by increasing numbers of larvae of *Nassa reticulata*. Finally, in September to November, the number of specimens is reduced considerably, while the number of species attains its maximum, comprising the autumn spawning, i. e., larvae of *Alvania punctura, Alvania abyssicola, Onoba vitrea, Coecum glabrum, Natica montagui, Eulimella nitidissima*, and scattered specimens of several other larval *Pyramidellidae*. All these larvae disappear during November, and from December to March or early April a pronounced minimum occurs, comprising only a few larvae of *Nassa reticulata* and *Aporrhais pes pelecani*, and some few laggards of *Littorina* larvae. In the winter months it was often seen that not a single larval Prosobranch was present in a main series (10 vertical hauls).

Thus, within a single year we have three distinct occurrences of Prosobranch larvae: spring larvae, summer larvae, and autumn larvae, of which only the summer larvae are present in sufficient numbers to constitute a real maximum in the plankton. In spite of these three "seasons" it will be seen that larvae of *Nassa reticulata* are among the first larvae in the spring and among the last larvae in the winter, occurring during all the intermediate months. As was also the case with the Polychaetes with a long season of larval occurrence (cf. p. 143), *Nassa reticulata* has a wide vertical distribution in the Sound, occurring in Baltic water as well as in Kattegat water. The Baltic water population will spawn early in the year, the Kattegat water population later on, according to the season at which the optimal temperatures for spawning are reached.

The pelagic Prosobranch larvae examined in our main series during the three years with exact counts, viz. from Ven 13,602 (in 45 main series) and from Helsingør 7,303 (in 20 main series), totalling 20,900 larvae, are distributed as follows:

	Off Ven	Off Helsingør	Total
Lacuna divaricata	1.0 %	2.6 %	1.6 %
Littorina littorea	81.0 -	58.0 -	72.6 -
Rissoa inconspicua	6.1 -	1.7 -	4.6 -
Other *Rissoidae*	0.7 -	3.1 -	1.6 -
Coecum glabrum	0.1 -	0.6 -	0.3 -
Bittium reticulatum	1.4 -	6.9 -	3.5 -
Pyramidellidae	0.2 -	0.3 -	0.3 -
Aporrhais pes pelecani	0.7 -	2.2 -	0.9 -
Naticidae	0.0 -	0.4 -	0.2 -
Nassa reticulata	5.5 -	18.9 -	10.3 -
Larvae of other Prosobranchs	3.3 -	5.3 -	4.1 -
	100.0 %	100.0 %	100.0 %

Thus, nearly three-fourth of all the Prosobranch larvae in the Sound belong to *Littorina littorea*, which is the absolutely dominant species. Next in dominance is *Nassa reticulata* with about 10 per cent. Then follow: *Rissoa inconspicua* with 4.6 per cent, *Bittium reticulatum* with 3.5 per cent, and *Lacuna divaricata* with 1.6 per cent. These five species together constitute 92.6 per cent of all the Prosobranch larvae in the Sound. The remaining 7.4 per cent are distributed over a great many different species all of little importance in the plankton. Interesting is the fact that the larvae of *Hydrobia ulvae*, the adults of which are by far the commonest Prosobranchs within the Sound, are nearly absent from our main series. The remarks on this species on p. 185 would show that the pelagic stage is somewhat reduced, but the nearly total absence of these larvae from the main series seems to show that the pelagic life must be extremely short. The larvae of for instance *Turritella communis* are also rare in the plankton (cf. p. 189) in spite of the relative high frequency of the adults, and here, also, the absence or paucity of larvae in our main series may be explained by their shortened pelagic life.

Among the Prosobranch larvae with a long pelagic life it seems possible to distinguish roughly between those which are derived from infauna parents and epifauna parents respectively. The following genera and species are regarded as infauna Prosobranchs with pelagic larvae in the Sound: *Onoba, Coecum, Eulima, Eulimella, Aporrhais, Natica*, and *Nassa reticulata*; and as epifauna Prosobranchs with pelagic larvae: *Acmaea, Lacuna, Littorina, Alvania, Rissoa, Bittium, Triphora, Odostomia, Velutina, Nassa pygmaea, N. incrassata*, and *Bela trevelyana*.

The quantitative occurrence of larvae belonging to these two groups is as follows:

Ven plankton		Helsingør plankton		Average for both stations	
Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna
1600 larvae = 6.5 %	23292 larvae = 93.5 %	3533 larvae = 25.0 %	10535 larvae = 75.0 %	5133 larvae = 13.0 %	33827 larvae = 87.0 %

Thus four-fifths to nine-tenths of the larvae found are derived from epifauna parents, which is in good agreement with the fact that *Littorina littorea* is the dominant larva in the plankton, and that *Nassa reticulata* is the only infauna species with pelagic larvae which is really frequent in the adult stage in the Sound. The other infauna Prosobranchs of common occurrence, viz. *Hydrobia ulvae* and *Turritella communis*, have, as mentioned above, a reduced pelagic life.

Only the most primitive groups of Prosobranchs spawn their eggs freely in the water, thus, in the Sound *Acmaea virginea*, *Helcion pellucidum*, and *Gibbula cineraria*. Other genera spawn their eggs in a gelatinous layer of different type and shape attached to a substratum, e. g. *Acmaea testudinalis*, *Gibbula tumida*, *Lacuna*, *Littorina obtusata*, *Bittium reticulatum*, some *Pyramidellidae*, and *Aporrhais*. These gelatinous egg ribbons may be incrusted with sand, e. g. in the *Naticidae*. Most other Prosobranchs deposit their eggs in cocoons or capsules of different shape, normally attached to a substratum. This is known for *Littorina littorea*, the *Rissoidae*, the *Hydrobiidae*, *Coecum*, *Triphora*, *Scala*, *Pelseneeria*, *Eulimella nitidissima*, *Capulus*, *Trophon*, *Nucella*, *Sipho*, *Neptunea*, *Buccinum*, *Nassa*, *Bela*, *Philbertia*, and *Mangelia*. A few forms are viviparous, viz. *Littorina saxatilis*, and *Hydrobia jenkinsi*. The eggs imbedded in a gelatinous layer or in cocoons or capsules will normally remain within this shelter until the crawling stage or — if they have a pelagic stage — until the larvae are fully developed veligers able to feed on the plankton as soon as they have been hatched out. While, therefore, the eggs shed freely in the water may be carried to other areas of the sea before reaching the veliger stage, the veligers hatching from egg masses or egg capsules will appear in the area in which they were spawned by their parents. The *Littorina littorea* larvae, finally, belong to an intermediate category, because their egg capsules are free, not adhering to any substratum. It seems probable, however, that most of these capsules in the Sound normally lie on the bottom. This assumption is supported by the fact that their occurrence in the plankton, which is normally rather sparse in the Sound, is considerably increased after at gale, by which they may be whirled up from the bottom. As, furthermore, the development inside the capsule only takes about six days in *Littorina littorea* (cf. p. 174), it may be expected that several of the larvae of this species originate from the Sound itself or the adjacent areas.

This supposition is supported by the fact that young just hatched larvae of this species are very frequent in the Sound. Also several other species of Prosobranch larvae occur in all stages of development in the Sound, the newly or just hatched young being often in the majority, e. g. those of *Alvania abyssicola*, *Rissoa sarsi*, *Coecum glabrum*, *Bittium reticulatum*, and *Nassa reticulata*. Hence it seems likely that a very large percentage of the larvae taken in our main series originate from parents in the Sound proper or the adjacent areas. This is in good agreement with the conditions found for most of the Polychaete larvae in the Sound, but in opposition to the conditions found for the Echinoderm larvae. Most of the larvae of this group found were large individuals just ready to metamorphose and no doubt originating from parents in the Kattegat (cf. p. 363). However, also the Prosobranch larvae in the Sound include species which occur only or mainly in large specimens nearly ready to metamorphose. This is for instance the case with the larvae of *Alvania punctura, Eulimella nitidissima, Aporrhais pes pelecani,* and *Natica montagui,* which should accordingly be regarded as "drift larvae" from the Kattegat.

Prosobranch larvae are in general fairly resistant to changes in the salinity and the temperature. When the fresh plankton from our main series was taken to the laboratory in Dewar vessels, the Echinoderm larvae were usually the first to die together with the young *Trochophores* of Polychaetes. The older Polychaete larvae are much more resistant, but the highest degree of resistance is found among the larvae of Gastropods and Lamellibranchs, which, withdrawn in their shells, may reduce a sudden change in the salinity to a rather slow osmotic process. Withdrawn in their shells with a reduced metabolism, they seem also to be capable of enduring rather considerable changes in the temperature, and observations from Helsingør have further shown that larvae of *Nassa reticulata* may swim lively about for several days in a glass dish with a higher temperature than found in the Sound and without any food (cf. this paper p. 459).

The duration of the pelagic life is discussed in detail on pp. 451—457. From this discussion it seems to appear that the Prosobranch larvae from northern seas, which are reared in nature or under laboratory conditions very like natural conditions, will take on an average two to four (five) weeks to pass from fertilisation to metamorphosis if spawned in the warm season. Examples are: *Rissoa membranacea* ("about 3 weeks or less"), *Nassa reticulata* (2 to 3 weeks), *Littorina littorea* (about 4 (to 5) weeks), *Bittium reticulatum* (about 3 weeks). This seems to be in good agreement with the time taken by other pelagic larvae of invertebrates within the same season.

All the Prosobranch larvae known from the Sound seem to feed exclusively on phytoplankton, and the literature and the calculations given on p. 447 seem to show that the phytoplankton organisms used as food may range within a theoretical maximum diameter of 5 to 45 μ. A large number of larvae have been reared to or even through the metamorphosis, feeding on *Nitzschia* (3 × 30 μ) and *Thalassiosira* (largest diameter 20 μ), while larger diatoms of the genera *Chaetoceras* or *Coscinodiscus* are of no use as food.

The Prosobranch larvae play a rather essential part as food for other marine animals. Among their enemies may be mentioned: young herrings (*Clupea harengus*), young specimens of garfish (*Belone acus*) and even adult specimens of mackerel (*Scomber scomber*), adult specimens of *Mytilus edulis, Balanus perforatus, Sagartia viduata,* and *Scyphistoma*'s of *Aurelia aurita* (concerning the literature on and discussions of these observations cf. pp. 467—471).

Summary of Discussion.

Sixty-nine species of Prosobranchs are known from the Sound as adults, larvae, or both. The larval development is known for 61 of them: 2 viviparous (and non-pelagic), 19 with a non-pelagic development, 5 with a short pelagic life, 0 with pelagic, lecithotrophic larvae, and 35 with a long pelagic, planktotrophic larval life. In the bottom stage the Prosobranchs constitute about 4 per cent of all the invertebrate specimens with pelagic larvae of the infauna, and about 10 per cent if the epifauna is also included; in good agreement with this the larvae represent about 12.5 per cent of all the larval invertebrates found in the Sound plankton. The Prosobranch larvae hatch normally as fully developed veligers able to feed on the plankton; they are fairly resistant to changes in the salinity and temperature. The average number of eggs shed by a single female is unknown for most species, but seems not to be very large. — The larval seasons are: a spring spawning with *Lacuna divaricata*, *Rissoa sarsi*, *Aporrhais*, and a few larva of *Nassa reticulata*; a summer spawning (the only real maximum during the year) with larvae of *Littorina littorea* as dominants and smaller numbers of larvae of *Bittium reticulatum*, and an autumn spawning with larvae of *Nassa reticulata* as dominants and *Alvania*, *Onoba vitrea*, *Coecum*, *Natica montagui*, *Eulimella nitidissima*, and other *Pyramidellidae* as accompanying animals, decreasing in number during November, until — from December to March or early April — there is a pronounced minimum, lasting until the spring spawning. Larvae of *Nassa reticulata* may occur during all three spawning seasons, because the adults with their wide vertical range will spawn at different times in the Baltic water and the Kattegat water, according to the temperature maxima of these layers. The larvae of *Littorina littorea* constitute 72.6 per cent of all the Prosobranch larvae occurring in the Sound plankton; those of *Nassa reticulata* constitute 10.3 per cent, those of *Rissoa inconspicua* 4.6 per cent, those of *Bittium reticulatum* 3.5 per cent, and those of *Lacuna divaricata* 1.6 per cent. The remaining 7.4 per cent fall upon several species of little importance in the plankton. *Hydrobia ulvae* and *Turritella communis* have such a short pelagic life that they play no part at all in the plankton. Four-fifths to nine-tenths of all the larvae found are derived from infauna-parents, which is in good agreement with the distribution of the adults. Northern pelagic Prosobranch larvae will on an average take two to four weeks to pass from hatching to metamorphosis in the warm season. Several Prosobranchs feed exclusively on rather small phytoplankton organisms and serve as food for several other animals: Fishes, Actinians, Lamellibranchs, and Balanids.

8. Opisthobranchia.

The following authors have contributed to our knowledge of the distribution of the Opisthobranch fauna in the Sound: Ørsted (1844), Mørch (1871, all earlier literature cited and discussed), Collin (1880), Petersen (1888), and Lönnberg (1898, 1899). — Own observations from the last few years and kind information received from Mr. Per-Magnus Lovén and Mr. Erik Rasmussen have added four new species to the fauna hitherto not recorded from the Sound, viz. *Philine punctata*, *Jorunna tomentosa*, *Idulia coronata*, and *Dendronotus robustus*. Thus, at present the fauna comprises 11 species of Tectibranchs, 3 species of Ascoglossids, and 27 species of Nudibranchs, that is to say, 41 species of Opisthobranchs are known from the Sound.

In this paper the Tectibranchs and Ascoglossids have been dealt with at length, while the Nudibranchs have only been summarily treated.

General Remarks on the Larvae and the Reproduction of Tectibranchs.

The spawn and the early stages of development have been described for several Tectibranchs, but very little is known so far about the Tectibranch larvae in the plankton. Various authors have described and figured the veligers of *Philine aperta* and *P. punctata* (see these species). Mazzarelli (1893), Saunders & Poole (1910), Moritz (1936), Thorson (1940 b), and other authors have described and partly figured young pelagic larvae of *Aplysia*; Mazzarelli (1906) has described and figured young larvae of *Actaeon tornatilis*, *Bulla striata*, *Gastero-*

pteron meckeli, and *Doridium tricoloratum*, BERRILL (1931) has examined and sketched the eggs and larvae of *Bulla hydatis*; THORSON (1940b) describes the spawn and young larvae of *Solidula solidulus*, LEGENDRE (1905) has dealt with the eggs and larvae of *Acera bullata*, and ERIK RASMUSSEN (1944) describes and figures the spawn and hatching larvae of *Retusa truncatula*.

The only Tectibranch larva which, as far as I know, has been observed during its whole larval development is that of *Philine aperta*. The newly hatched larvae known for other forms are so little characteristic that they are of no value if we try to identify older larvae from the plankton.

During our working up of the larvae from the Sound it turned out that a couple of larvae with sinistral, helicoid shells and dextrally organised animals, which had hitherto been referred to the *Pyramidellidae* (cf. these pp. 199—212), actually belonged to the Tectibranchs. A common feature of the sinistral larval shells in the *Pyramidellidae* seems to be that they are more or less scalariform, while those of the Tectibranchs are helicoid. Thus, for instance, some of the larvae referred by MARIE LEBOUR (1936, p. II, fig. 21) to the *Pyramidellidae* have proved to be typical Tectibranch larvae.

Among these sinistral Tectibranch larvae, those of the genus *Philine* were easily referred to the right genus, because the elongated last whorl, the wide mouth of the larval shell, and the large jet-black excretory organ had already been described as characteristic features of the larvae of *Philine*. As, furthermore, the larvae of *Philine aperta*, *P. scabra*, and *P. punctata* are known from the Sound undergoing metamorphosis and in young bottom stages, their identity was easily established. The larva of *Acera bullata* — though of quite a different type — is also easily recognisable, and the whole metamorphosis could be followed in our bottle-collectors off Ven. Four more species of Tectibranch larvae, which do not belong to *Philine* or to *Acera*, occur in the Sound plankton, and for three of these four species we know the young bottom stages, in which the typical dextral Tectibranch shells had already developed. The next step, then, was to have the larval shells and these young bottom stages identified in detail.

A most successful collaboration with Dr. H. LEMCHE, Copenhagen, helped to solve also these questions. Dr. LEMCHE, studying the morphology of northern and arctic Tectibranchs, as a part of this work made some very fine preparations of the apices of all the Danish species available. When the whorls of the dried bottom stages are broken through, and the callus is removed from the apex, which in most species is hidden in the interior of the shell, the previous larval shell is distinctly seen. Dr. LEMCHE found that the type of larval shell attached to the apex is a good indication of the type of larval life in these species: A large clumsy apex is a safe criterion for a non-pelagic development, while a distinct larval shell with regular whorls indicates a pelagic larval life. The larval shells of the latter type found on the apices of the adults proved to be so well preserved that direct comparisons with the drawings of Tectibranch larvae from the Sound warranted an identification with a very large degree of certainty. Using these methods, we succeeded in referring all the species of Tectibranch larvae known from the Danish plankton to their adult species. The reasons leading to these identifications are given below under the descriptions of the individual species. The apices dissected out of the adult stages will later be discussed and figured in a special paper by Dr. H. LEMCHE, whom I here wish to thank for good help and inciting collaboration.

A. Tectibranchia.

Actaeon tornatilis Linné. Northern part of the Sound, rather rare.

Reproduction: A. Literature. Mazzarelli (1906, p. 29) describes and figures the young larvae of this species from Naples: Breeding in May. The larvae hatch out eight to twelve days after the eggs have been spawned. The larvae are blind on hatching, 116 μ across the shell, and 170 μ across the expanded velum.

B. Own remarks. Plankton taken off Helsingør on $^{25}/_{10}$-41 contained two larvae (fig. 144 A—C), which according to their sinistral helicoid shells were typical Tectibranchs. The larval shell, 320 to 350 μ in largest diameter, of $1^{1}/_{2}$ to $1^{3}/_{4}$ whorls, had a moderately elevated, pale yellowish, helicoid spire, and the last whorl had a very characteristic shape. The mouth is rather narrow and is very obliquely situated as though belonging to another longitudinal axis than the preceding part of the shell. When seen from the apex the shell is quite oval, the liver is yellowish-brown, and there are two small black eyes. The larvae had died before being examined, and the first signs of dissolution were seen. No trace of pigmentation could be observed.

According to the obliquenes of the mouth it might be taken for granted that the larval shell were united with the following adult whorls at a more oblique angle than known

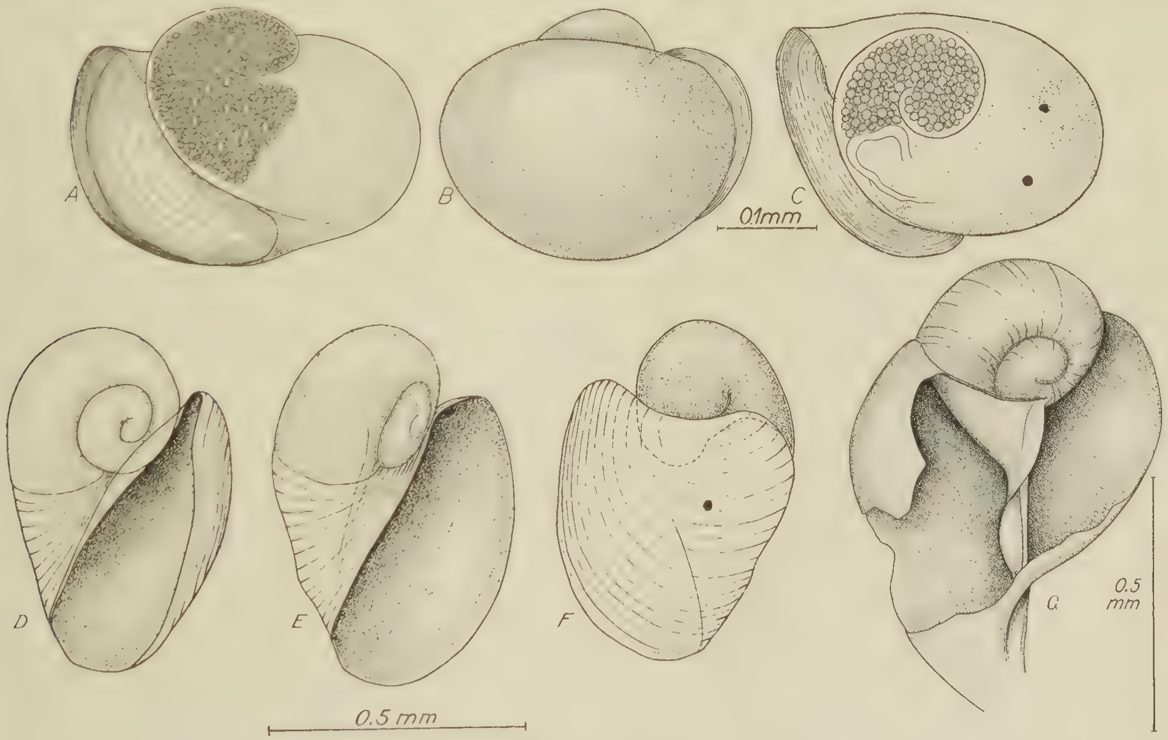


Fig. 144 A-G. *Actaeon tornatilis* Linné. — *A* to *C*. Old larva presumably belonging to this species (see the text pp. 247—248). From plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{25}/_{10}$-1941 (drawn dead on $^{26}/_{10}$). Seen from the mouth (A), the dorsal side (B), and the top of the apex (C). — *D* to *F*. Youngest bottom stage known. Caught floating in the plankton between Hellebæk and Kulla Gunnarstorp, depth 30-0 m, on $^{11}/_{11}$-1941 (drawn dead on $^{14}/_{11}$). Seen from the mouth (i. e. left side of the larval shell, (D)), from the ventro-lateral side (i. e. dorso-lateral side of the larval shell (E)), and from the dorsal side (i. e. right side of the larval shell (F)). — *G*. Apex of adult shell from Læsø Rende (N. Kattegat), dissected out and placed at my disposal by Dr. H. Lemche.

for the species of *Retusa* and *Diaphana*. -- On $^{11}/_{11}$-41, i. e. three weeks after the larvae were found, a young metamorphosed bottom stage, still floating in the plankton, was found off Helsingor (fig. 144 D—F). Three-fourths of the first dextral adult whorl had already formed, and the larval shell was situated on the top of this and at an angle quite different from that of the other genera of Danish Tectibranchs. A comparison with the Tectibranch apices (fig. 144 G) dissected out by Dr. H. LEMCHE showed that the larvae and the young bottom stage belonged to *Actaeon tornatilis*. The young bottom stage had two black eyes and the same yellowish colour of the larval shell as was found in the pelagic larvae, while the adult shell is white.

Retusa (Utriculus) truncatula (BRUGIÈRE). Northern part of the Sound, rare.

Reproduction: A. Literature. MEYER & MÖBIUS (1865, p. 88) mention eggs from the Bay of Kiel laid in an aquarium in May. The white eggs, about 80 in number, are laid in a transparent lump of slime, 3 mm across and 1.3 mm high (no figures). ERIK RASMUSSEN (1944) from the Isefjord, Denmark, gives a detailed account (with good figures) of the breeding, egg masses, embryos, and newly hatched larvae. His results may be summarised as follows: Spawning in May to July. Often several spawns are crowded together. The spawning of an egg mass takes about one hour. About 500—700 eggs, white and shaped like a hen's egg, each of them 190 to 210 μ across the egg membrane and 100 μ across the egg cell proper, are laid in irregular windings in a colourless, round or oval mucus, 3 to 5 mm across. The whole development from spawning to hatching took $5^1/_2$ days at 20° C. The hatching veligers, 150 μ in longest diameter of the shell, have sinistral shells, a bilobed velum, a pointed, ciliated foot, and one black eye only. The larvae are transparent to yellowish, with a dark reddish pigment on the mantle, and the organisation of the larva is dextral in spite of its sinistral shell.

B. Own remarks. Spawning was observed in aquaria at Nyborg (Great Belt) on $^{12-14}/_7$-28 by Dr. H. LEMCHE, who kindly placed his notes and a number of fixed egg masses at my disposal. The eggs are laid in a string one by one (fig. 145 A—B), but this string is coiled up and surrounded by a thin colourless slime. The whole spawn is thus a globular to sausage-shaped gelatinous lump, $1^1/_2$ mm across, which is fastened by its sticky surface to small fragments of stone or detritus on the bottom. The individual egg capsule contains one embryo only and is often somewhat oval (largest diameter 140 μ). Embryos in the first stages of cleaving are about 75 to 80 μ across. Fig. 145 A shows a spawn of medium size, which contained 446 embryos. Older embryos were not observed.

The adults are rare in the Sound, and no larvae were found in the plankton here which could be referred to this species. The adults are very abundant in the western part of the Limfjord (N. Jutland), and during a stay there in the summer of 1940 I had a good possibility of clearing up its development and identifying the larva. A young metamorphosed bottom stage (fig. 145 G—H) with one half adult whorl was found in a sample taken off Nykobing Mors, depth 6 m, on $^7/_7$-40, together with adults of *Retusa truncatula*. The sinistral larval shell with very irregularly increasing whorls, owing to which the spire was oblique (in contrast to that of *Diaphana*), was distinctly seen on the top of the young bottom stage and was easily identified with a couple of larvae normally occurring in the plankton in the same locality. Thus it was found that the larvae as well as the young bottom stage belonged to a Tectibranch, probably of the genus *Retusa*. As *R. truncatula* is abundant and is the only species of *Retusa* occurring in the area mentioned which is known to have pelagic larvae, everything suggested this species. The final confirmation of this supposition was found by comparing the sketches made with the apex of *R. truncatula* dissected out by Dr. H. LEMCHE, which both as regards the larval shell and the first adult whorl agreed entirely with the young bottom stage from the Limfjord.

The older larvae (fig. 145 C—D) have sinistral, helicoid, transparent shells (longest diameter 310 to 330 μ) of $1\,{}^{1}/_{4}$ to $1\,{}^{1}/_{2}$ whorls. The whorls increase so rapidly in size that the apex of the larval shell is no more found in the centre, when the larval shell is seen from above.

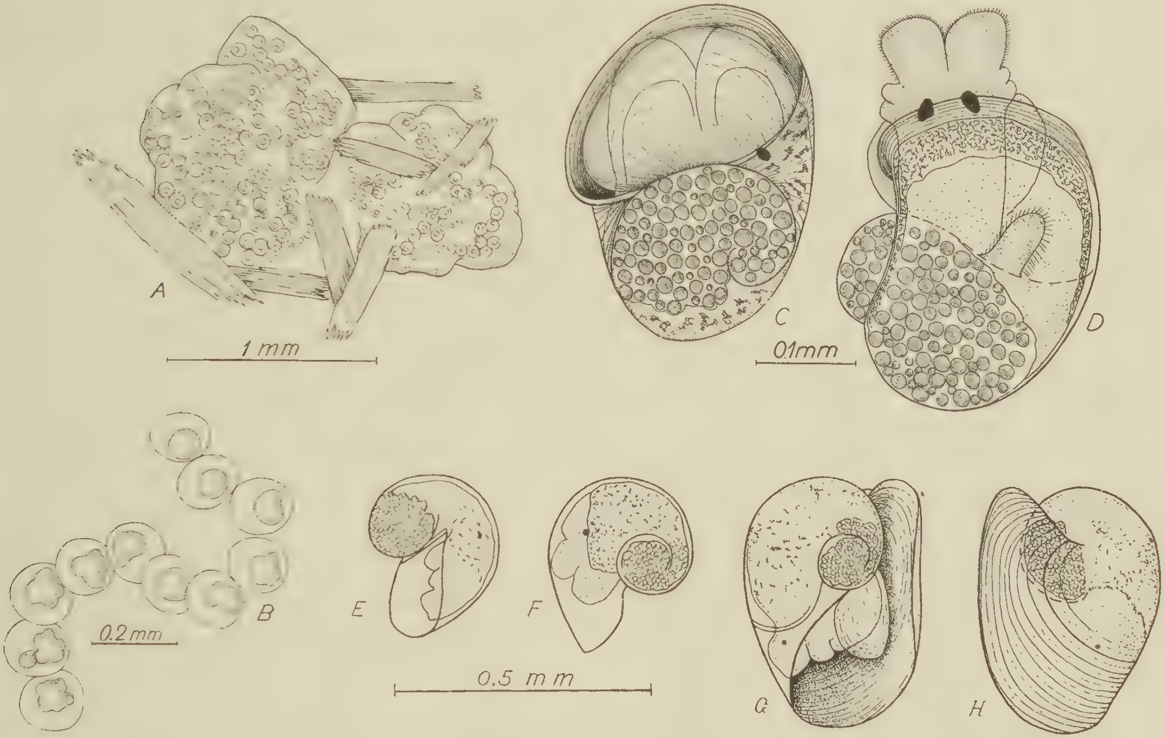


Fig. 145 A-H. *Retusa truncatula* (BRUG.). Egg mass and development. — *A*. Egg mass laid in aquarium in Nyborg (Great Belt) on $^{12}/_{7}$-1928 (drawn from an egg mass fixed in formalin). — *B*. Section of the egg cord contained in the egg mass fig. 145 A with young embryos. — *C* and *D*. Old larvae from plankton off Nykøbing Mors (the Limfjord, NW. Jutland), depth 1-0 m, caught and drawn from life on $^{9}/_{7}$-1940. Seen from the ventral side (C), and from the dorsal side (D, ready to metamorphose, crawling on the bottom, with reduced velum). — *E* and *F*. Oldest planktonic larvae found (dates and locality as fig. C and D). Seen from the ventro-lateral side (E), and from the left side (F). — *G* and *H*. Youngest bottom stage known. Taken off Nykøbing Mors, depth 6 m, caught and drawn from life on $^{7}/_{7}$-1940. Seen from the ventral side (G, left side of the larval shell), and from the dorsal side (H).

The liver is yellowish-brown, and there is a rather broad border of a purplish-blue pigment along the margin and the sides of the mantle. In some specimens brownish-black grains of pigment are seen in the body wall in front of the liver. The velum is bilobed, rather small, and the larvae sketched here had already lost their velum and were able to crawl. Two large black eyes. The young bottom stage (fig. 145 G—H) had, on its top, a larval shell which agreed entirely with those from the plankton. The size of the shell with the apex removed from the centre, the colour of the liver, and the distribution of the pigment are precisely as in the larva. The heart is now very large, and the operculum is still present. The boundary between the larval shell and the first adult whorl is distinct.

Retusa (Cylichna) umbilicata (Montagu) (= **R. nitidula** (Lovén)). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. Unknown.

B. Own remarks. Plankton from the Sound contains an abundance of larvae (fig. 146 A–C) which in their whole appearance bear a fairly close resemblance to those from the Limfjord referred to *Retusa truncatula*. The larvae from the Sound, however, show a few distinct deviations from the *truncatula* larvae in the Limfjord. The shell in the older larva is larger, 370 to 375 μ, with a somewhat more elevated spire, and the purplish-black pigmentation is distributed over the whole mantle and large parts of the body wall. The liver is yellowish-brown, the velum small, bilobed, and colourless (somewhat reduced in the larvae figured), and there are two large black eyes. The mouth of the shell is very wide (cf. fig. 146 A). The larvae in question are abundant in the Sound and probably belong to a species of common occurrence there. Thus only *Retusa umbilicata* could come into consideration, and a comparison between the larval shell and the apex of adult shells dissected out by Dr. H. Lemche has confirmed this supposition.

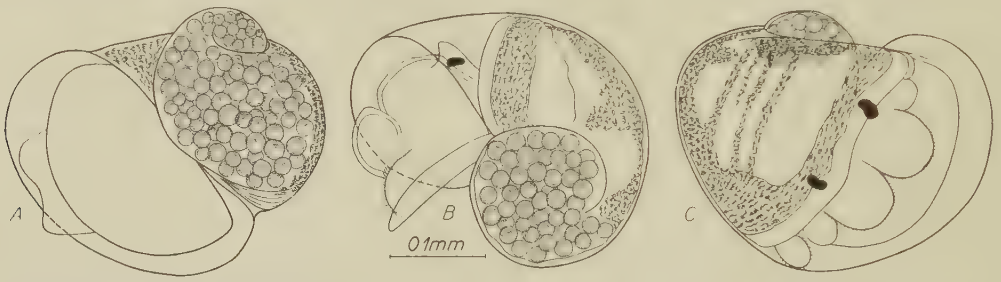


Fig. 146 A-C. *Retusa* (*Cylichna*) *umbilicata* (Montagu). — Older larvae from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{19}/_{7}$-1939, seen from the ventral side (A), the left side (B), and the dorsal side (C).

The larvae of *Retusa umbilicata* are known from the plankton taken off Ven during the period from late May (earliest find in the year $^{17}/_{5}$-39) to December or early January (latest finds $^{6}/_{12}$-36 and $^{7}/_{1}$-39). The season at Helsingør is from June ($^{4}/_{6}$-42) to December ($^{2}/_{12}$-41). In this period the larvae were found very regularly in the plankton, being present in nearly all the main series. The maximum number of larvae per main series (10 vertical plankton hauls) were: 160 (on $^{15}/_{7}$-39); 81 (on $^{21}/_{8}$-37); about 60 (on $^{3}/_{7}$-39); 52 ($^{6}/_{6}$-38), and 50 ($^{2}/_{8}$-37) all taken off Ven. The maximum numbers off Helsingør were: 44 (on $^{11}/_{11}$-41 and $^{25}/_{7}$-42). One to fifteen larvae per main series are the usual numbers for the season. Larvae in all sizes and stages of development are present. A large number of them originate from parents living in the Sound itself. — Young, just metamorphosed bottom stages were not met with.

Retusa obtusa (Montagu) (= **Utriculus pertenuis** Sars). Reported by Mørch from the waters off Copenhagen, not found later.

Reproduction: Unknown in the literature. No observations from the Sound. According to the preparations of the apex undertaken by Dr. Lemche the species has, no doubt, a non-pelagic development.

Diaphana hyalina TURTON. Northern and middle parts of the Sound, not rare.

Reproduction: A. Literature. Unknown.

B. Own remarks. Plankton from the Sound includes some regularly twined sinistral-shelled larvae of Tectibranchs, which have a characteristic reddish-brown tint along the suture and on the columella (fig. 147A—B). A comparison with the apex dissected out of adults of the Danish species of Tectibranchs showed that the larva in question was so strikingly similar to the larval shell on the apex of *Diaphana hyalina* (cf. fig. 147G) that there was not the slightest doubt as to their identity. The regularly increasing whorls, the glossy transparent shell, and even the reddish-brown tint along the suture found in the pelagic larva were found again in the larval shell on top of the adult apex.

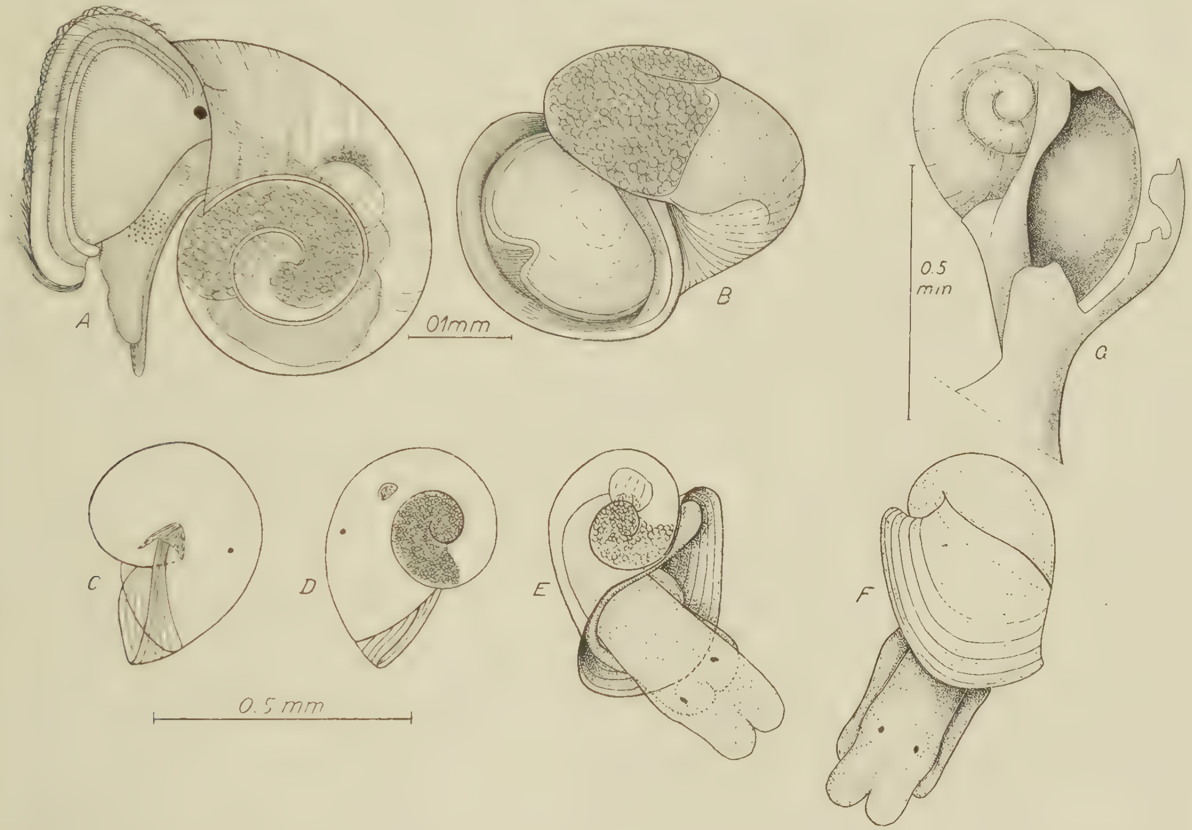


Fig. 147 A-G. *Diaphana hyalina* TURTON. — *A* and *B*. Old larvae from plankton off Frederikshavn (NW. Kattegat), depth 4-5 m, caught and drawn from life on $^{1}/_{7}$-1937. Seen from the left side (A, the animal stretched out), and the ventral side (B, the animal withdrawn). — *C* and *D*. Youngest bottom stage found with the first small trace of the adult shell. From a bottle-collector exposed off Ven, depth 16 m, from $^{7}/_{7}$-$^{28}/_{8}$-1939 (drawn when just dead on $^{31}/_{8}$-1939). Seen from the right side (C), and from the left side (D). — *E* and *F*. Young bottom stage, which metamorphosed in an aquarium on Ven. Taken in plankton off Frederikshavn, on $^{27}/_{7}$-1939, and drawn from life after metamorphosis on $^{2}/_{8}$-1939. Seen from the mouth of the adult shell (i. e. the left side of the larval shell (E)), and from the dorsal side of the adult shell, (i. e. the right side of the larval shell (F)). — *G*. Apex of adult specimen from Brandsø Bredning, depth 14-21 m, dissected out and placed at my disposal by Dr. H. LEMCHE.

In the oldest stage of the larva of *Diaphana hyalina* (fig. 147A—B) the largest diameter is 350 to 380 μ across the helicoid shell. The liver is reddish-brown, the excretory organ orange-red (not known for any other Danish Tectibranch larva), and there are small dark spots of pigment on the foot. Two black eyes, distinct statocysts, and a rather large bilobed velum. See further the characteristics mentioned above.

Our larva was first discovered in plankton off Frederikshavn (N.E. Jutland) on $^{1}/_{7}$-37, and was later found off Ven on the following dates: $^{4}/_{9}$-37 (9 spms. in all stages of development); $^{12}/_{9}$-37 (9 spms. in all stages); $^{9}/_{10}$-37 (1 large spm.); $^{13}/_{8}$-38 (1 large spm.); $^{24}/_{9}$-38 (3 spms.); $^{8}/_{10}$-38 (1 large spm.); $^{12}/_{11}$-38 (1 large spm.); $^{4}/_{6}$-39 (12 young spms.); $^{17}/_{6}$-39 (8 spms. in all stages), and off Helsingør on: $^{7}/_{10}$-41 (1 large spm.); $^{4}/_{6}$-42 (2 young spms.); $^{20}/_{6}$-42 (1 young spm.); $^{6}/_{7}$-42 (15 spms. in all stages); $^{18}/_{7}$-42 (1 large spm.); $^{25}/_{7}$-42 (1 large spm.), and $^{7}/_{8}$-42 (4 spms. in all stages). The main season is thus summer and autumn. The young larvae found show that the species grows considerably during its pelagic life and that the stock originates at least partially from parents in the neighbourhood. — Bottle collectors exposed near Ven, at a depth of 16 m, from $^{7}/_{7}$-39 to $^{28}/_{8}$-39, contained several young crawling stages of this species (fig. 147 C—D), the adult whorls of which had just commenced to form. Older stages undergoing metamorphosis were not found in the Sound, but the stage sketched in fig. 147 E—F, taken near Frederikshavn on $^{2}/_{8}$-39, has the same regularly increasing whorls and the same large heart as were found in the larva dealt with here, and should, no doubt, be referred to the same species.

Acera bullata Müller. Throughout the Sound, common locally.

Reproduction: A. Literature. The egg masses are described by Meyer & Möbius (1865). Eggs were laid in aquaria in January, and were abundant in the Bay of Kiel in May-June. Yellowish-white eggs, surrounded by a rather tough colourless jelly, form a gelatinous egg string 2 to 3 mm thick and 7 to 8 cm long. The individual egg mass contains about a thousand eggs. Legendre (1905) mentions from Concarneau several specimens in copulation, and egg masses in August to September. Copulation takes usually place between 10 and 12 o'clock in the morning in a shady place. Up to six (hermaphroditic) animals may mate at the same time, forming a chain, one animal behind the other. Each specimen copulates several times. Spawning about eleven days after copulation (at 15°—18° C). Legendre confirms the number of eggs per egg string mentioned by Meyer & Möbius (l. c.), viz. about one thousand.

B. Own remarks. Egg masses of *Acera* are known from the Sound from the following localities and dates, viz. off Ven: $^{9}/_{7}$-36 (16—17 m, on red and brown algae); $^{18}/_{8}$-36; $^{30}/_{6}$-39 (10—12 m, numerous egg masses); $^{2}/_{7}$-39 (several females spawning in aquarium), and off Helsingør: $^{11}/_{7}$-41 (depth $^{1}/_{2}$ to 1 m, 2 egg masses); off Malmö $^{15}/_{6}$-39 (depth 14 m, 2 egg masses, H. Brattström leg.); Staffans Bank $^{30}/_{6}$-36 (depth 15 m, 12 egg masses, Brattström leg.); N.E. of Saltholm $^{4}/_{9}$-36 (2 egg masses on *Laminaria*, Brattström leg.). — In addition egg masses are present from the Isefjord: $^{6}/_{5}$-1890 (several egg masses); $^{28}/_{5}$-26 (1 egg mass on *Zostera*), and $^{5}/_{7}$-24 (large numbers, Blegvad leg.). Besides the few dates noted from Ven the egg masses are known to occur throughout the summer in the brown and red algal zones in a rather considerable number.

Spawning was observed (in aquarium) on $^{2}/_{7}$-39 (cf. fig. 148 A). The female, which was attached to a lump of red algae, moved slowly forwards. The egg string appeared in the genital aperture on the right side of the animal and adhered to the algae. The following part of the egg string, which, when emerging from the oviduct, was forced backwards into a groove between the shell and the right border of the mantle, adhered to the algae in long coils. The jelly com-

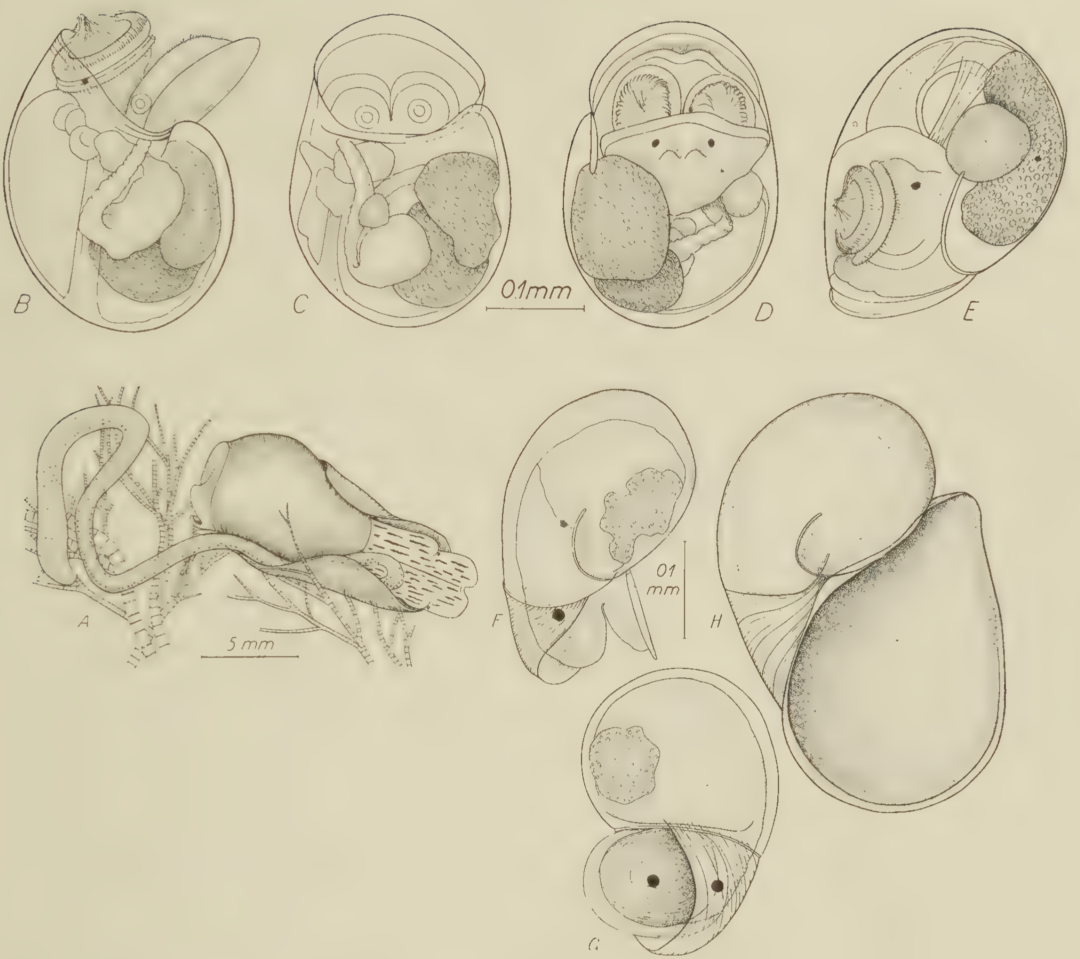


Fig. 148 A-H. *Acera bullata* Müller. — Reproduction and development. — *A*. Female in oviposition, using red algae as a substratum for the egg cord. Taken off Ven, on $^{2}/_{7}$-1939 and drawn from life in aquarium the same day. — *B* to *E*. Planktonic larvae just hatched from the egg mass, seen from the right side (B), the ventral side (C), the dorsal side (D) and the left side (E). From egg mass taken in the Little Belt, depth 20 m, on $^{29}/_{7}$-1944 (the larvae hatched and were drawn from life on $^{30}/_{7}$-1944) — .*F* and *G*. Youngest bottom stage found. The first trace of the adult dextral shell is seen; the velum is reduced. Seen from the left side (F) and the right side (G) of the larval shell. From a bottle-collector exposed off Ven, depth 16 m, from $^{5}/_{7}$ to $^{27}/_{8}$-1939 (drawn on $^{28}/_{8}$-1939 shortly after death). — *H*. Empty shell of young bottom stage with the first dextral whorl formed, seen from the mouth of the adult shell (i. e. from the left side of the larval shell). From a bottle-collector exposed off Ven, depth 16 m, from $^{5}/_{7}$-$^{23}/_{8}$-1939.

menced to swell in the part of the egg mass first laid even before the whole spawn had been produced. — Late embryos were dissected out from older egg masses, and on comparing them with the planktonic larvae, the development was easily followed until and during metamorphosis. The pelagic larvae (fig. 148 B—E) have nearly the same type of shell as is known from larvae of Tergipedids (cf. p. 269), but the *Acera* larvae are larger, 300—375 μ in longest diameter, and more robust. Their growth in the plankton — if they grow at all — is inconsiderable just as in the Nudibranch larvae, and on this point they differ from the other Tectibranchs, which feed and grow rapidly in the plankton. The shell is pale yellowish. The liver is yellowish-green, coarsely granulated; the other parts of the body have often a

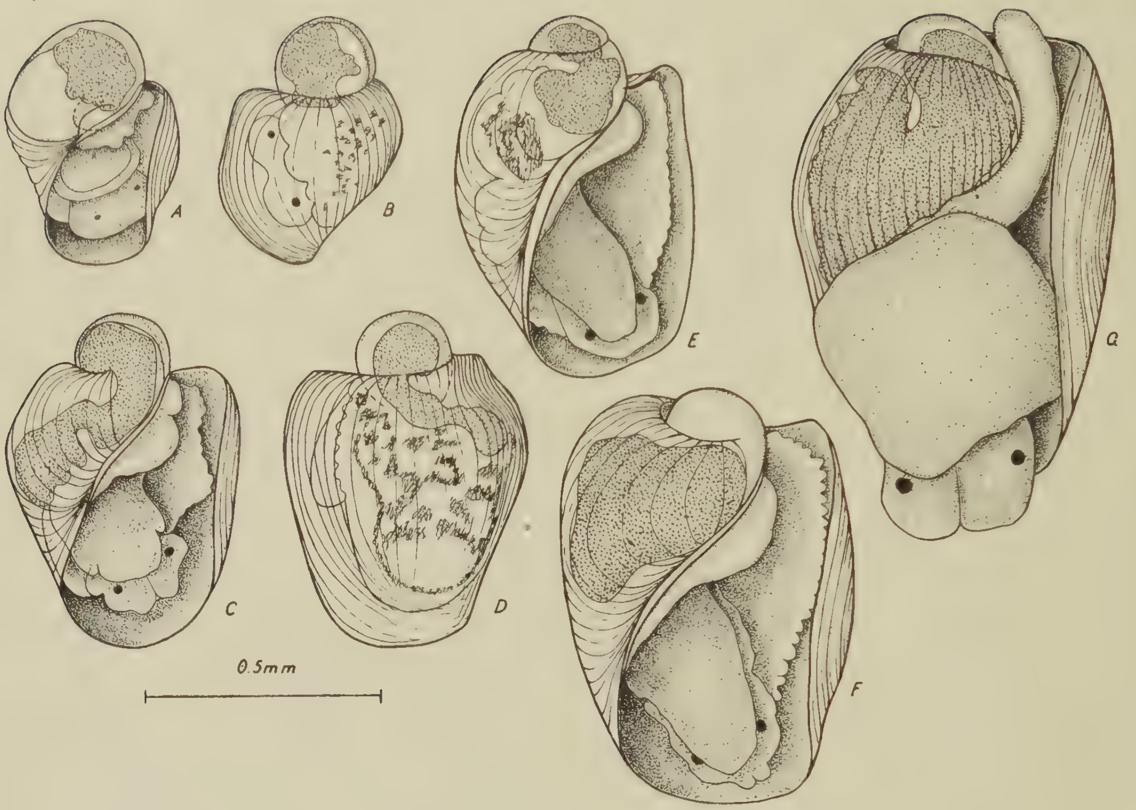


Fig. 149 A-G. *Acera bullata* Müller. — Young bottom stages in different phases of development, seen from the mouth (A-C-E-F and G) and from the dorsal side (B and D). From bottle-collectors exposed off Ven, depth 16 m, from $^{5}/_{7}$-$^{23}/_{8}$ and $^{7}/_{7}$-$^{29}/_{8}$-1939 respectively (drawn from life on $^{25}/_{8}$ (fig. E-F), and on $^{30}/_{8}$-1939 (figs. A-B-C-D and G)).

very pale purplish tint. Two black eyes, two distinct statocysts, operculum, and a small, bilobed velum.

A few larvae may be found in the plankton of the Sound in all the months of the year, but the main season is from early May to December, with a maximum occurrence in July, August, and September. The maximum numbers of larvae per main series (10 vertical hauls) were off Ven: 125 larvae (on $^{17}/_{7}$-38); 250 larvae (on $^{13}/_{8}$-38), and off Helsingør: 96 larvae ($^{6}/_{7}$-42); 52 larvae ($^{17}/_{8}$-42), and 100 larvae (on $^{5}/_{9}$-42). Thus the larvae of this species are common, but never dominant, members of the plankton. The inconsiderable growth indicates that the larvae stay only for a short time in the water masses. It is not impossible that during the investigations near Ven in 1936—37 larvae of this species have been confused with large Nudibranch larvae (e. g. those of *Embletonia pallida* and those seen in fig. 160, p. 271), but our identifications made during the last few years are quite certain.

A series of bottle collectors exposed near Ven, at a depth of 16 m, from $^{5-7}/_{7}$-39 to $^{23-29}/_{8}$-39 contained young of *Acera bullata* in all stages of metamorphosis, and hence it was possible to sketch and observe the whole development from the pelagic larval stage to a stage in which the young had nearly all the characters of the adults (figs. 148F—H, 149). It turned out that when the first whorl succeeding the larval whorl has formed, the sinistral character of the larval shell is distinct; in the youngest bottom stages the larval shell is seen as a sinistral apex on the top of the dextral shell (fig. 148 H). The first whorl but one is horn-coloured and widens quickly, thus covering part of the larval shell, which is still more covered by the following whorls. The liver of the young bottom stages very soon attains a brownish-black colour, and the surface of the mantle a reddish-brown pigmentation (fig. 149), which in older stages is also found on the head. The growth of the young bottom stages seems to be rapid. Young specimens, which on metamorphosis had a longest diameter of the shell of 375 μ, hardly 7 weeks later had attained a height of the shell of 1080 μ.

Philine aperta (Linné). Throughout the Sound, common at greater depths.

Reproduction: A. Literature. Meyer & Möbius (1865, with figs.), Guiart (1901), and Lacaze-Duthiers & Pruvot (1888) have described the early development before hatching. Boutan (1902) and Mazzarelli (1906) have figured the newly hatched larvae, and Brown (1934) has given a detailed study with several figures of the pelagic larvae until metamorphosis. This is a summary of his data: Copulation probably only once in a lifetime. The spawn "is a jelly-like mass, normally from two to three inches long by almost one inch wide". The oval egg capsules, 140 μ long, form a string, which "coils at random inside the egg mass, and the egg string is surrounded by a tough, gelatinous envelope, which tails off into a strand at each end of the egg-ribbon", thus being anchored to the mud. — The larva hatches 8—10 days after the spawning, and is a characteristic blind veliger. The shell has a wide mouth, a simple whorl in one plane, and measures 90 μ across. The larva is colourless apart from the yellowish stomach and liver, and a reddish-brown border of pigment along the margin of the rather small bilobed velum. A large jet black excretory organ is found on the right side. Foot and large operculum are present, but no eyes. Older larvae, 140 μ across the shell, actively feeding on the plankton, have two black eyes and, besides the pigment border along the margin, a pair of small semicircular areas of pigment on the central area of the anterior face of the velum. In the oldest pelagic larvae (190 μ across the shell) the tentacles have already formed and the foot has developed a flat undersurface. Larvae, 220 μ across the shell, have already lost their velum, and the foot has shed the operculum. The tentacles have fusen and become flattened; the young animal is in the crawling stage.

B. Own remarks. The figures of Brown (l. c.) are very clear; they aim at showing the development within the "type Philine", but do not enable us to identify the larvae in the plankton. Accordingly they are schematic to a certain extent. They enable us to refer a planktonic larva to the genus *Philine*, but hardly to decide which species of *Philine* we have before us. As, however, four species of *Philine* are known in the adult stage from the Sound, and as three further species are known from other Danish waters, it was necessary to find out the characteristics of the larvae of each single species.

Egg masses of *Philine aperta* were taken in the Sound off the Hittarp-reef, on $^{28}/_{7}$-41 (depth 25 m, very large spawn), off Hellebæk on $^{12}/_{9}$-41 (depth 35 m, 1 spawn, $1^{3}/_{4}$ cm long, 1 cm wide, and further a $1^{1}/_{2}$ cm long strand. Quite young eggs inside), and several egg masses were found off Ven in August 1936. Spawns of this species have further been observed at Frederikshavn (N.W. Kattegat) on $^{8}/_{7}$-35 (depth 20—25 m, 1 medium-sized spawn), and on $^{20}/_{7}$-37 (depth 14–16 m, 1 medium-sized spawn). The main season for spawning is thus July to September. At Nykøbing Mors (the Limfjord, N.W. Jutland) several large egg masses were taken on $^{1}/_{7}$-40 in quite shallow water. Two of these (fig. 150 A—B) were carefully examined. They measured 2.2 × 1.7 cm and 3.9 × 1.6 cm respectively (the strands not included) and each of them contained an egg string with numerous rather regular coils. A count of a rather large number of windings showed that the two egg masses in question contained about 25,000 and 50,000 egg capsules respectively, each with a large rotating embryo (fig. 150 C—D). As it may be supposed that each female spawns several times each season, the number of larvae produced per female per year must be estimated to be very large. The larvae shown in fig. 150 D, sketched inside the capsules, are just ready to hatch and have a colourless shell of hardly one whorl and are twined in one plane. The longest diameter of the shell is 120 μ, i. e. much longer than stated by BROWN from Scotland. Apart from the large black excretory organ these hatching larvae are quite colourless. Older larvae are sketched in fig. 150 E—G. The colourless shell, which is now distinctly sinistral with an elongated, widened last whorl, measures 340 to 400 μ in largest diameter, i. e. a size far exceeding that of the metamorphosing larvae from Scotland (viz. 220 μ). The liver is reddish-brown, and there is a large jet-black excretory organ on the right side. The rather large velum is faintly four-lobed and has a border and an inner semicircle of reddish-brown pigment on the velum, as already described by BROWN. Sometimes this pigment is absent on the larvae in the Sound, while the larvae are often provided with a reddish-brown border of pigment along the margin of the mantle. Black pigment is often seen across the stomach. Two black eyes, two statocysts, and a strongly beating heart are distinct. Larvae in this stage are nearly ready to metamorphose. They spend a day or two in the swimming-crawling stage; then the velar cilia are cast off, and the larva begins to crawl on the bottom. The following stages (fig. 150 H—Q) were taken in bottle-collectors exposed near Ven, depth 16 m, from $^{5}/_{7}$-39 to $^{29}/_{8}$-39. From the margin of the sinistral larval shell, which forms the apex of the adult shell, the new dextral whorls, which are very wide, smooth, and without any structure at all, will grow out. The black excretory organ and the brown pigment along the border of the mantle as well as the two black eyes are distinct. The front part of the body is yellowish-white, with pale brown pigment spots. Still older bottom stages (600 μ across the shell, not figured) have a rather conspicuous reddish-brown pigmentation on the head and the front part of the body. Liver yellowish-rose-coloured.

The larvae of *Philine aperta* have their main season in the plankton from early July to early November. The maximum numbers of larvae per main series (10 vertical hauls) found near Ven were as follows: 74 (on $^{17}/_{7}$-38); 60 (on $^{9}/_{8}$-37); c. 100 (on $^{13}/_{8}$-38); 72 (on $^{12}/_{9}$-37); 130 (on $^{24}/_{9}$-37); 87 (on $^{9}/_{10}$-37), and 32 (on $^{23}/_{10}$-37), and off Helsingor: 58 ($^{18}/_{7}$-42); 720 ($^{25}/_{7}$-42); 120 ($^{17}/_{8}$-42); 170 ($^{5}/_{9}$-42); 125 ($^{7}/_{10}$-41), and 170 ($^{11}/_{11}$-41). In October-November nearly all the larvae found were in the oldest pelagic stage. A few larvae may occur in December-January, and also a few larvae from March, April, May, and June have been referred to this species. On certain occassions *Philine* larvae were the dominating larval Gastropods

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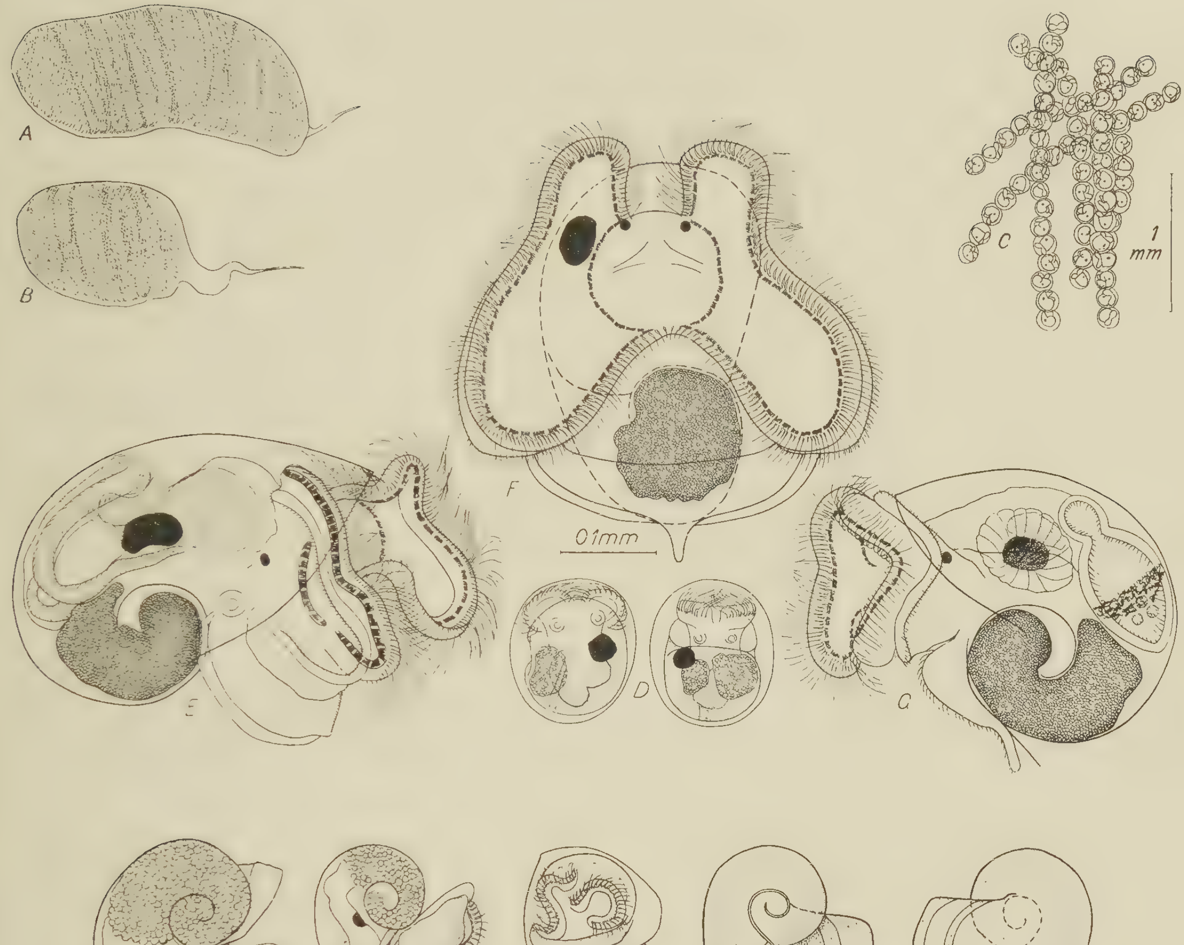
Fig. 150 A-Q. *Philine aperta* (LINNÉ). Egg masses and development. — *A* and *B*. Egg masses with about 50000 and 25000 rotating embryos respectively. Natural size. Taken near the shore (10 cm water) off Nykobing Mors (the Limfjord) on $^{10}/_{7}$-1940 (drawn from life the same day). — *C*. Egg strings from the egg mass fig. A more highly magnified (drawn from life on $^{10}/_{7}$-1940. — *D*. Two capsules from this string with embryos ready to hatch (drawn from life on $^{10}/_{7}$-1940) · *E*, *F* and *G*. Old larvae from plankton off Nykøbing Mors, depth 2-0 m, on $^{4}/_{7}$-1940 (drawn from life the same day), seen from the right side (E), the front (F), and the left side (G). The velum is only partially extended. — *H* and *I*. Larvae in swimming-crawling stage seen from the left side (H), and from the dorso-lateral side (I). From a bottle-collector, exposed off Ven, depth 16 m, from $^{5}/_{7}$ to $^{2}/_{9}$-1939 (drawn from life on $^{3}/_{9}$-1939). *K* to *Q*. Young metamorphosed bottom stages from a bottle-collector exposed off Ven, depth 16 m, from $^{5}/_{7}$ to $^{29}/_{8}$-1939 (figs. K, L, O, P and Q are drawn from life on $^{30}/_{8}$-1939). *K* and *L* youngest bottom stages found seen from the left side (K), and from the right side (L). — *M* and *N*. Empty shell of young metamorphosed bottom stage seen from the left side (M) and from the right side (N). — *O*, *P* and *Q*. Stages a few days older than figs. K to N, seen from the dorsal side(O), the mouth (P, left side of larval shell), and from the left side of the adult shell (Q).


A
B
C
1 mm
F
01mm
E
D
G
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I
M
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L
O
P
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0.5mm

in the plankton, e. g. off Ven on $^{12-13}/_{8}$-37 and $^{26-27}/_{9}$-36. They grew rapidly in the plankton, and their pelagic life seems to be long. - Some of the larvae in the samples from the period from 1936 to the summer of 1937 may have been confused with those of *Philine scabra* (see this species).

Philine scabra Müller. Middle and northern parts of the Sound, rather common at fairly great depths.

Reproduction: A. Literature. Unknown.

B. Own remarks. At Frederikshavn (N.W. Kattegat) an egg mass was taken at a depth of 14 m on $^{22}/_{7}$-36 which should in all probability be referred to this species. Each spawn contains a much smaller number of eggs than the spawns of *Philine aperta*. The eggs are laid in a globular jelly, 2 mm across, and the spawn is anchored to the mud by a 11 mm long strand (fig. 151 A—B). The spawn contained one rotating embryo in each capsule (no twins), it was placed in a glass dish, where the first embryos hatched on the same evening. In larvae one day old (fig. 152 A) the largest diameter of the shell was 90 μ, i. e. a much smaller size than found for hatching larvae of *Philine aperta* in Danish seas (see this species). The excretory organ, which was carmine in the embryos, was quite black in the pelagic larvae, which are without the slightest trace of a pigment-border on the velum — a fact which is in good agreement with the data stated for older larvae of the species in question. The larvae which were placed in a glass dish with zoospores of *Enteromorpha* died on $^{25}/_{7}$. — Spawns of an entirely similar appearance were found in some localities off Ven in which the adults were abundant: on $^{7}/_{8}$-36 (14—17 m, 1 spawn, 2 × 3 mm across the jelly, with a strand 7 mm long, and containing young eggs), on $^{13}/_{8}$-38 (1 spawn), and on $^{21}/_{8}$-36 (fig. 151 B, 17 m, 2 spawns, $1^{1}/_{4}$—2 mm across the jelly, with $1^{1}/_{2}$—3 mm long strands). The eggs of one of the last-mentioned spawns measured 105 μ across the egg membrane and 65 μ across the egg cell proper. The last two spawns contained 50 undeveloped eggs and 70 rotating embryos respectively (*Philine aperta* has 25,000 to 50,000 eggs per spawn!).

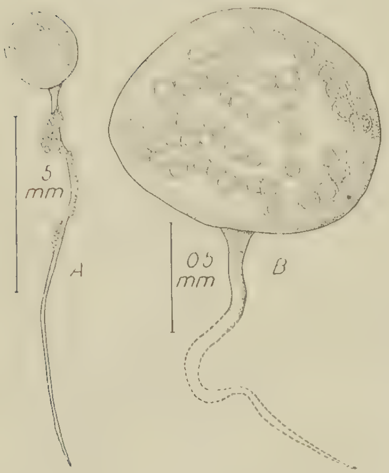
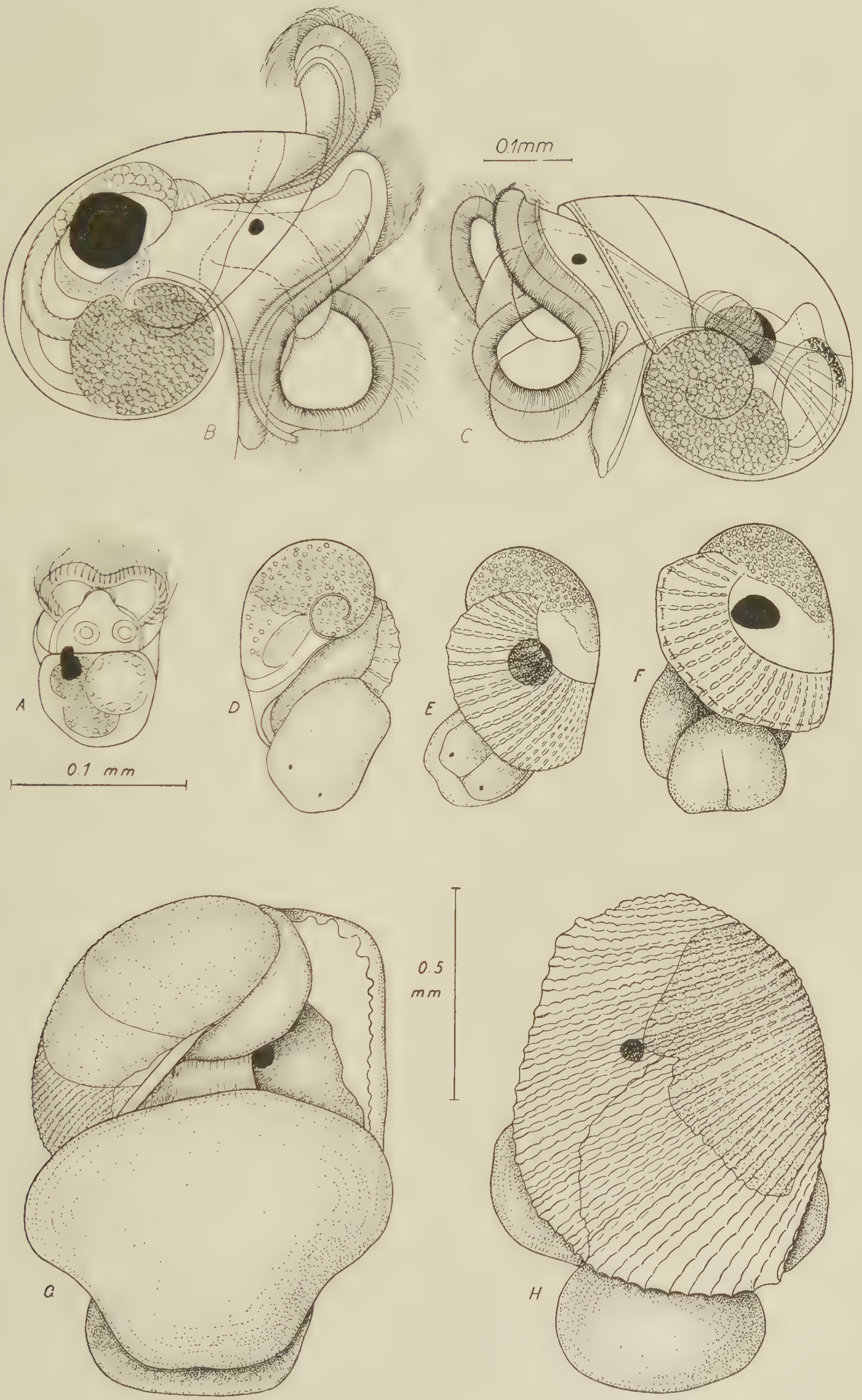


Fig. 151 A-B. *Philine scabra* Müller. Egg masses. — *A*. Egg mass with large, rotating embryos taken off Frederikshavn (NW. Kattegat), depth 14 m, muddy bottom, on $^{22}/_{7}$-1936 (drawn from life the same day). — *B*. Egg mass with young eggs at higher magnification. Taken off Ven, depth 17 m, muddy bottom, on $^{21}/_{8}$-1936 (drawn from life the same day).

The older larvae (fig. 152 B—C) were identified by means of the different metamorphosing stages found in our bottle collectors. The main characteristic, which led to their identification, was a huge, jet-black excretory organ present in the youngest crawling stages and later on also found in the larvae. In the stage just before they leave the plankton these larvae have a colourless sinistral shell, 400—440 μ across, i. e. somewhat larger than the

Fig. 152 A-H. *Philine scabra* Müller. Development. — *A*. Larva just hatched from the egg mass fig. 151 A. — *B* and *C*. Old larvae from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{10}/_{8}$-1940. Seen from the right side (B), and the left side (C). — *D*, *E* and *F*. Young, just metamorphosed bottom stages, from a bottle collector exposed off Ven, depth 16 m, from $^{17}/_{9}$ to $^{21}/_{10}$-1939 (drawn from life on $^{23}/_{10}$-1939). Seen from the mouth (D, left side of the larval shell), and from the dorso-lateral side (E, F). — *G* and *H*. Somewhat older bottom stages from a bottle-collector exposed off Ven, depth 16 m, from $^{5}/_{7}$ to $^{2}/_{9}$-1939 (drawn from life on $^{3}/_{9}$-1939). Seen from the mouth (G) and from the back (H).


0.1mm
B
C
A
D
E
F
0.1 mm
0.5 mm
G
H

oldest larvae of *Philine aperta*. The shell has the same elongated shape of the last whorl and the same wide mouth as in *Philine aperta*, and may hardly be distinguished from that of the latter species. The larva in question, however, is very characteristic. The excretory organ, 80 μ across, is much larger than that of the larva of *Philine aperta*. The velum is also larger, faintly four-lobed, and without any trace of pigment. However, a pale brown border of pigment is found along the margin of the mantle. The liver is yellowish-brown; there is a black pigmentation on part of the stomach-wall. Intestine, heart, black eyes, and operculum distinct. Statocysts were not seen.

Bottle collectors exposed off Ven at a depth of 16 m from $^{17}/_{9}$-39 to $^{21}/_{10}$-39 contained several young bottom stages of this species (fig. 152 D—H). In the same bottle collectors similar stages of *Philine aperta* were also abundant, a fact which allowed of a direct comparison. Even the first whorl succeeding the larval whorl has the slender shape and the pearl-string-like structure typical of the adult *Philine scabra* (fig. 152 E, F, H), while *P. aperta* in the same stage has a much broader shell with a quite smooth surface. The liver is yellowish-brown, and there is a very pale border of brown pigment along the margin of the mantle. The animal itself is white with two small black eyes.

Larvae of this species are known from the plankton taken off Ven on: $^{13}/_{8}$-38; $^{22}/_{8}$-38, and $^{10}/_{8}$-40, and off Helsingør on: $^{25}/_{10}$-41 (6 large spms.); $^{11}/_{11}$-41 (1 large spm.), and $^{17}/_{8}$-42 (7 large spms.). They are much less abundant than the larvae of *P. aperta*, and their occurrence seems to be restricted to the late summer and autumn. During the years 1936—37 the larvae may probably now and then have been confused with the *aperta* larvae, and in younger stages they will habitually always be difficult to separate from these, while sketches and measurements or a careful examination will give certain results also for the young stages.

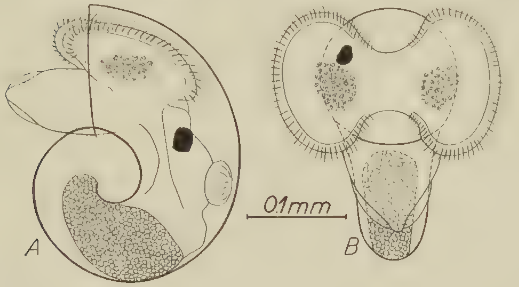


Fig. 153 A-B. Larva presumably belonging to *Philine quadrata* Wood. (See the text pp. 260-261). From plankton off Ven, depth 18-0 m, caught and drawn from life on $^{24}/_{10}$-1937. Seen from the left side (A), and from the ventral side (B). (From sketches made by mag. sc. Erik Smidt).

The fact that each spawn of *Philine scabra* contains from 50—70 eggs, and each spawn of *Philine aperta* from 25,000 to 50,000 eggs, as also the fact that the larvae of *P. scabra* have a pelagic larval life just as long or even longer than the larvae of *P. aperta*, i. e. just as large a "waste" in the pelagic stage, seems to show that the individual female of *Philine scabra* must produce a very large number of spawns every year in order to maintain its population.

Philine quadrata Wood. Old records from Hellebæk and Ven, rare.

Reproduction: A. Literature. Unknown.

B. Own remarks. Dr. H. Lemche has dissected out the larval whorls which form the apex of the adult shell, and which are found nearly intact in the middle of this adult shell surrounded by all the following whorls. His preparations showed that the larval shell of this species was flat, twined in one plane only, entirely like a *Planorbis*, and not in a sinistral spiral as in the other Danish species of *Philine*. Our plankton includes a larva (fig. 153 A—B) which clearly belongs to the genus *Philine*, and which has a planorbiform shell. This larva was found off Ven on: $^{24}/_{10}$-37 (1 spm.) and $^{1}/_{7}$-38 (7 spms.), and the same larva was found in plankton off Frederikshavn (N.W. Kattegat) on $^{30}/_{7}$-39. Older larvae have unfortunately not been figured. A rather young larva is seen in fig. 153 A—B. The shell, 295 μ across, with $1^{1}/_{3}$

whorls, is colourless, quite planorbiform, and with a circular mouth. The liver is yellowish-brown, there is a large jet-black excretory organ of the type characteristic of the genus *Philine.* The bilobed velum has strong cilia, and in the middle of each of the rounded lobes there is a very distinct and characteristic spot of reddish-purple pigment. Heart and operculum, but no eyes or statocysts, are seen. The larva is a typical *Philine,* and as the larva of *P. aperta* and *P. scabra* are already known, it seems most reasonable to refer the present larva to *Philine quadrata,* especially as the larval shell agrees fairly well with that found on the apex of the adults.

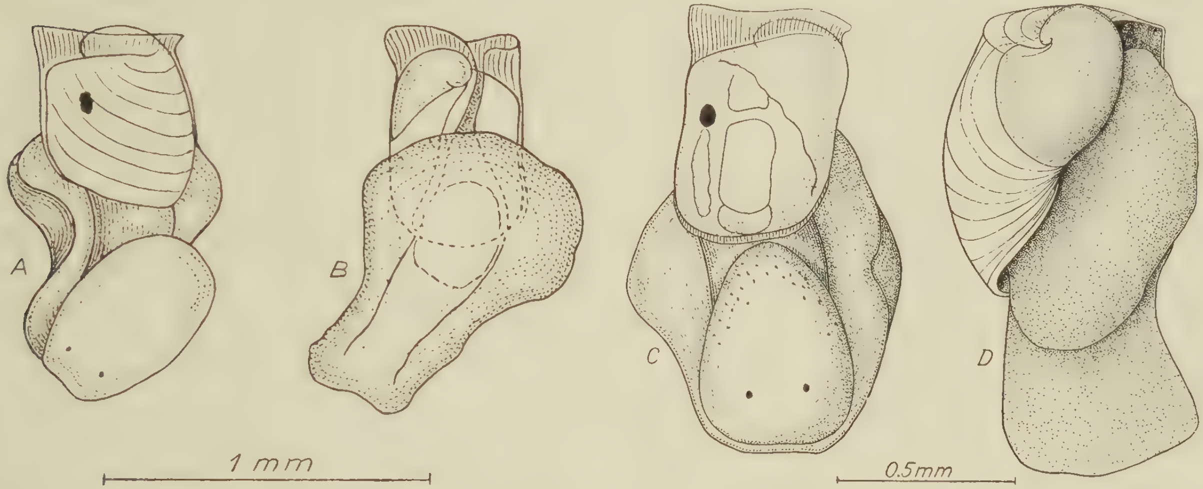


Fig. 154 A-D. Young bottom stages presumably belonging to *Philine punctata* Clark. — *A* to *C*. Young bottom stage floating in plankton off Ven, depth 18-0 m, caught and drawn from life on $^{8}/_{8}$-1938. Seen from the dorso-lateral side (A), the ventral side (B, larval shell distinct), and from the dorsal side (C, drawn at higher magnification). - *D*. Older bottom stage from clay bottom off Ven, depth 17 m, (detritus sampler), caught and drawn from life on $^{21}/_{8}$-1936. Seen from the ventral side. Larval shell distinct.

Philine punctata Clark. No records are at hand from the Sound.

Reproduction: A. Literature. Pelseneer (1911) has described the egg mass and figured the larvae from Wimereux. The spawn is globular, gelatinous, 2 mm across with the eggs arranged in transverse rows inside. The spawn is attached to a stone just below the low-water mark. The egg size is not given. The larvae just hatched, 85 μ across the shell, have the same wide shell-mouth and the same large black excretory organ as are known from larvae of other Philinids. As, however, the larvae reared by Pelseneer all died a few days after hatching, and as his sketches give no features which may serve to distinguish this larva from those of other species of *Philine,* it is impossible to recognise the *Philine punctata* larva on the basis given here.

B. Own remarks. The larva is not known from our plankton, but may have been included in the group of "young larvae of *Philine sp.*" or confused with young larvae of *P. aperta* or *P. scabra.* Off Ven, however, a young metamorphosed *Philine* was taken in a vertical plankton haul on $^{8}/_{8}$-38 (fig. 154 A—C). The animal differed distinctly in appearence from that of young bottom stages of *Philine aperta* and *P. scabra* of the same size (see these species), and the larval shell (sinistral, not planorbiform, with a very wide mouth), which was still seen on the apex, was completely different from that found by Dr. Lemche on the apex of *Philine quadrata*. The narrow shape of the adult whorls, the collar-like brim of conchiolin protecting the larval shell on the apex, and a rather small, but distinct, black excretory organ seem to be the most characteristic features of the young stage. The animal is yellowish-white with small brown spots of pigment on the hindmost part of the cephalic lobe. Another young bottom stage was taken off Ven (depth 17 m, mud, fig. 154 D) on $^{21}/_{8}$-36 which was somewhat more advanced in development than the specimen mentioned above. The larval shell on the apex has the same shape (extremely wide mouth, only slightly twined), and the two larval shells are of nearly the same size, viz.: 400—480 μ across. The young animal from $^{21}/_{8}$ has, further, a keel on its transparent milky-white shell in just the same place in which the conchiolin-brim is seen in the younger specimen. This keel forms an angle on the outer lip of the shell. To all appearence these two young should be referred to one and the same species, and as *P. aperta*, *P. scabra*, and *P. quadrata* must be disregarded, only *P. punctata* (with *P. angulata*) and *P. pruinosa* may come into consideration. As *Philine pruinosa* has a quite different shape of the shell in older stages, it seems most reasonable to refer the young stages in question to *Philine punctata*. Dr. LEMCHE, who has carefully studied the systematic problems in the Tectibranchs, is of opinion that *P. angulata* should possibly be regarded as a variety — or perhaps as one of the sexes — of *Philine punctata*. The shell of this species bears a close resemblance to those of the young stages found here.

[**Aplysia punctata** CUVIER (= **A. rosea** RATHKE). Unknown from the Sound, but occurring, though not frequently, in the northern Kattegat and Skagerrak. Common along the Bohuslän coast.

Reproduction. A. Literature. The breeding habits and development of *A. punctata* have been dealt with by MAZZARELLI (1893, 1906), CARAZZI (1905), SAUNDERS and POOLE (1910), NORDGAARD (1912), COLGAN (1914) and NELLIE EALES (1921). Their results are briefly: Breeding season at Naples winter to early summer, at Plymouth spring and late summer, at Ireland spring, summer and autumn as late as November, at Norway spring. At Plymouth specimens going to spawn will migrate from greater to smaller depths. Breeding normally takes place at night. The hermaphroditic animals copulate in "chains" of three to five (up to ten) specimens. The lowermost individual acts as female only, the topmost as male only, and the intermediate ones function as male for the preceding and as female for the succeeding individual of the chain. The copulation lasts for several hours or even days. The animals may begin to spawn already during or immediately after copulation. The gelatinous egg cord, which is not extruded continuously, but in little spurts of about an inch, may be up to 18 m long and is attached to sea weed, Hydroids or Ascidians forming an orange or pink tangled mass. In one cord are numerous transparent egg cocoons each containing 3—7 or 6—10 eggs. The total number of eggs cocoons contained in a single cord is estimated at 30,000 (COLGAN), 80,000 (CARAZZI) to 108,000 (FISCHER according to EALES). The egg is "less than 100 μ in diameter" and takes — in April at Naples — a fortnight from fertilisation to hatching. All eggs develop into reddish-brown pelagic veligers without eyes. The older pelagic larval stages as well as the metamorphosing stages are unknown.

B. Own remarks. Adult specimens caught on $^{18}/_{8}$-1945 in the Gullmarfjord (Bohuslän, Swedish W. coast), depth 6 m, after several copulations spawned their first egg-strings on $^{20}/_{8}$-1945 at noon-tide. The egg-strings, examined half an hour later, contained several egg cocoons crowding densely side by side (fig. 155 A). The individual cocoon (fig. 155 B) contains several eggs, thus for twenty cocoons 8-8-8-9-9-9-9-9-9-9-9-10-10-10-10-10-11-11-11, and 12 eggs respectively, i. e. 9.5 eggs on an average per cocoon. One cm egg-string contains on an average 210 egg cocoons, i. e. about 2000 eggs or embryos per cm egg-string. A single egg-string will then normally comprise several hundred thousand eggs, and an egg string of 18 m length (as mentioned in the literature by Eales) will accordingly contain more than $3^1/_2$ millions of eggs or larvae. The yolky eggs ($85\ \mu$ across with a very thin egg membrane, fig. 155 C) are pink, the cocoons and the very tough slime surrounding them and forming the egg string are quite colourless, but the eggs give the whole string a pinkish colour. Each cocoon is connected with its neighbour cocoons by a thin string which shows the order in which the cocoons have been laid.

During the next week several egg strings were deposited, although none of them were complete. When, after 13 days absence, I returned to the Gullmarfjord on $^8/_9$-1945 several larvae had already hatched in the aquaria and several others were in the hatching stage. The larvae in the moment of hatching (fig. 155 D—H) have dark yellowish-brown shells of $1^1/_4$ whorl and with a characteristic "beaten structure". The columella is dark reddish-brown and so is the callus stretching from this columella along the inner part of the mouth. The swimming veliger is blind, with a hardly bilobed small velum, without a subvelum, but with medium-sized cilia. Two distinct statocysts were seen. — Older larvae were not seen.]

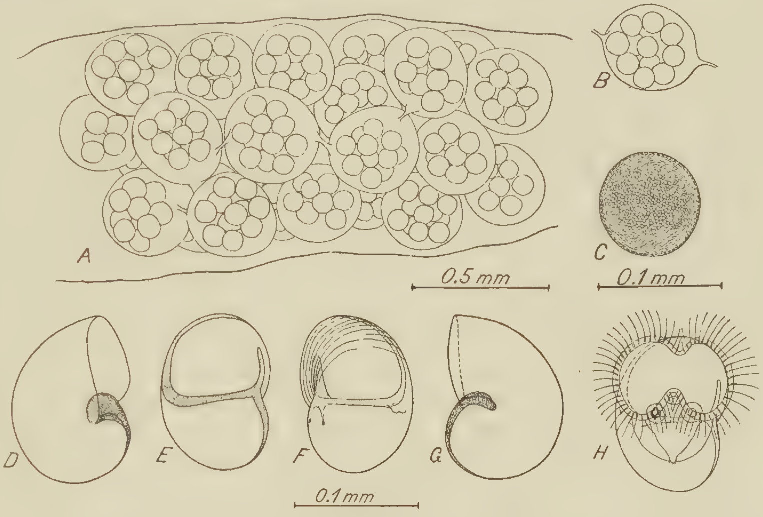


Fig. 155 A-H. *Aplysia punctata* Cuvier (= *A. rosea* Rathke). — Egg masses and larvae, spawned and reared in aquaria from parents caught in the Gullmarfjord (Bohuslän, Swedish W. coast) on $^{10}/_8$-1945. All figures drawn from life on the date given in brackets. — *A.* Section of new-spawned egg string. — *B.* Single egg cocoon. — *C.* Uncleaved egg (all drawn on $^{20}/_8$-1945). — *D* to *H.* Larvae in the hatching stage. Empty shells seen from the right side (D), the ventral side (E), the dorsal side (F), and the left side (G). — *H.* Swimming larva seen from the ventral side ($^8/_9$-1945).

Tylodina duebeni Lovén. One specimen, taken off Aalsgaarde in the northern part of the Sound by Collin in 1865. Not found later. This is the only record from the Danish seas.

Reproduction: Unknown in the literature. No observations from the Sound.

B. Ascoglossa.

Limapontia capitata (Müller). Throughout the Sound, rather common.

Reproduction: A. Literature. The egg masses have been described by Alder & Hancock (1845—1855) and Meyer & Möbius (1865, with figures), while Vestergaard & Thorson (1938) have described and figured egg masses as well as hatching larvae from the Danish waters. The egg masses laid on *Zostera* or on different algae (*Cladophora*, *Ectocarpus*) are globular or sausage-shaped, largest diameter 1 to 5 mm. Each egg mass consists of

10 to 450 small lemon-coloured eggs, 130 × 110 μ, formed like a hen's egg, and imbedded in a common, rather thick and resistant mass of jelly. Normally only one embryo is found per egg membrane, but twins may occur. At Frederikshavn (N.W. Kattegat, at 15°–17° C) the larvae were hatched 7–8 days after the fertilisation of the eggs. The newly hatched larvae, 100–110 μ across the colourless shell, have a colourless bilobed velum, a black excretory organ, black pigment around the mouth and in the pharynx, and a pale olive-green liver. Statocysts distinct, no eyes. Erik Smidt (1944) has figured the planktonic larvae from the Copenhagen harbour on the basis of our identifications from the Sound laboratory.

B. Own remarks. The newly hatched larvae described above (fig. 156 A—B) were searched for in summer plankton at Frederikshavn, but in vain, and accordingly it seemed likely that the pelagic stage was very short as in most other "Nudibranchs".—In plankton from the Sound a very characteristic larva occurred throughout the year. Its most typical features were: the sinistral shell, 290–320 μ across, the large, black excretory organ, and the black pigment on the bilobed velum, forming a figure like two black eyebrows (fig. 156 C—D). The liver was yellowish-green, eyes and statocysts were distinct. Older larvae now and then showed an intense purplish-black pigmentation on the outer surface of the body wall. In a few specimens the "eyebrow-pigment" on the velum was absent, but normally it is distinct and a good criterion.

During four years these larvae were noted down in our lists without being identified. During my stay by the Limfjord (N.W. Jutland) in July, 1940, larvae of this type occurred in large numbers in the plankton. On $^{6}/_{7}$-40 about a hundred of the oldest larvae in the swimming-crawling stages were selected out from the plankton and placed in glass dishes with carefully cleaned leaves of *Ulva*. On $^{9}/_{7}$-40 most of them had cast off their shells and turned out to be the young of *Limapontia capitata*. A larva still in its shell, but crawling and with a reduced velum, was placed under the microscope to be sketched (fig. 156 E), but already five minutes later the shell was discarded and the metamorphosis could be observed in all details. The first sign of an approaching metamorphosis is the reduction of the velum, which disappears entirely before the young leaves its shell. Just before the animal leaves the shell the operculum is also cast off. A few minutes after the larvae have left their shells, the bluntly-rounded hindmost part of the foot (fig. 156 E) changes into the adult acute shape (fig. 156 G), and the process on the foot, to which the operculum earlier adheared, disappears. A few days after metamorphosis the curved spiral shape of the body characteristic of larvae in their twined shells changes into the straight shape characteristic of the adults. Larvae in the stage of metamorphosis when leaving their shell (fig. 156 G-H) bear a close resemblance to the figure by Pelseneer (1899 b, pl. 27, fig. 14—17) of the young crawling stage of the closely related *Cenia cocksi*, which has a reduced development and leaves the shell inside the egg mass.

These larvae are very remarkable, because they feed on the plankton and grow considerably during their pelagic life. In contrast to this the "true Nudibranchs" (which see) mainly seem to be lecithotrophic and to have a short larval life. According to modern views, however, the *Ascoglossa* should be regarded as a transitional group between the Nudibranchs and the Tectibranchs, and a larval development like that found for *Limapontia* seems to indicate their close connection with the Tectibranchs, the larval development of which takes place in a quite similar way (see these species).

Larvae of *Limapontia capitata* are to be found in the plankton of the Sound in all the months of the year. Off Ven only a few specimens were met with in each main series (10 vertical hauls). The maximum numbers per main series in this locality were 27 larvae (on

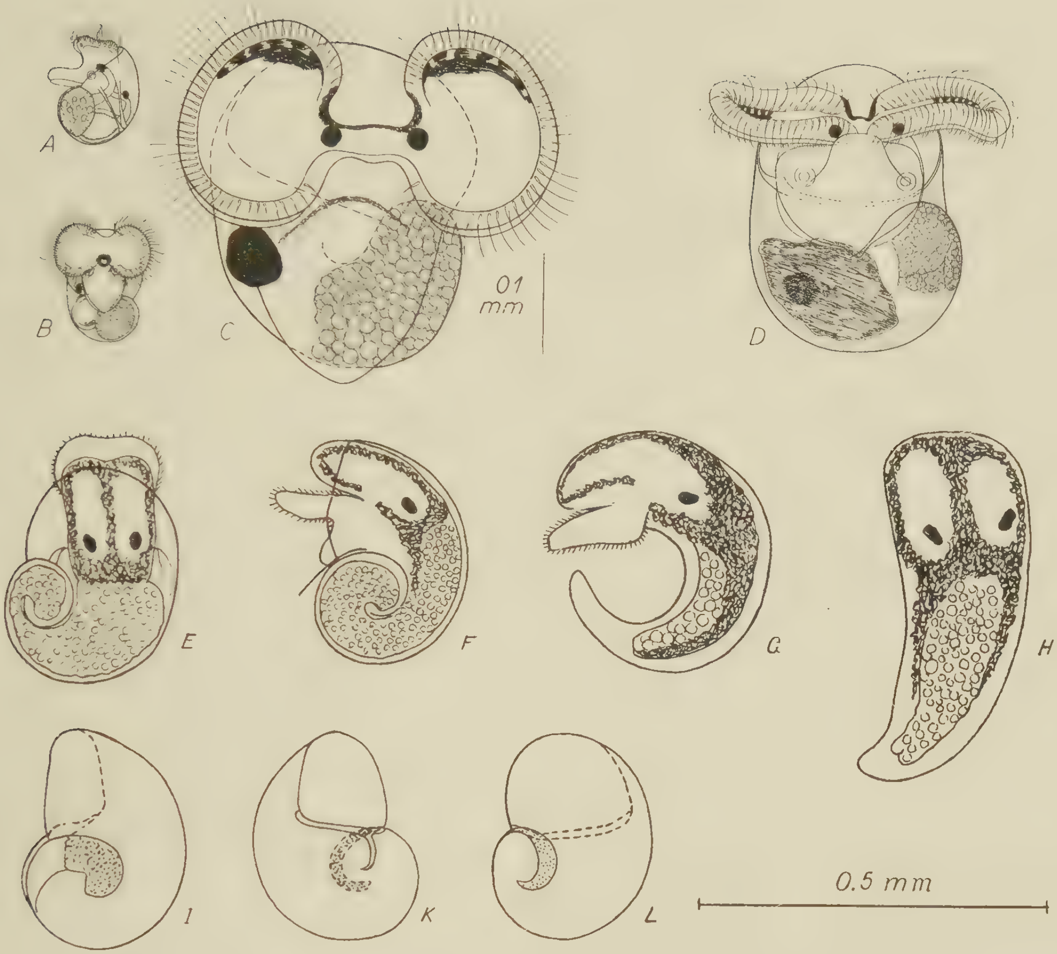


Fig. 156 A-L. *Limapontia capitata* (Müller). — Larval development and metamorphosis. — *A* and *B*. Planktonic larvae just hatched from the egg mass, seen from the left side (A) and from the ventral side (B). Taken in Ringkøbing Fjord (W. Jutland) and drawn from life in June 1937 (from Vestergaard and Thorson 1938). — *C*. Old larva from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{20}/_{10}$-1936. — *D*. Old larva, ca. 300 μ across the shell, from plankton off Nykøbing Mors, depth 2-0 m, caught and drawn from life on $^{2}/_{7}$-1940. — *E* to *F*. Larvae in the crawling stage just before metamorphosis with reduced velum, seen from the dorsal side (E) and from the left side (F). — *G*. Young bottom stage less than one day after metamorphosis, seen from the left side. The spiral shape of the body characteristic of the shelled veliger is still present; the operculum is thrown off. — *H*. Young bottom stage a day later than fig. G., seen from the dorsal side. — *I* to *L*. Empty larval shells cast off by the metamorphosing animals, seen from the left side (I), the right side (K), and the ventral side (L). The "pseudo-whorl" of the shell is intransparent in its innermost part. — Figs. E to L are drawn on $^{9-10}/_{7}$-1940 (figs. E to H from life). From animals kept in glass jars at Nykøbing Mors, where the whole metamorphosis was studied.

$^{9}/_{10}$-37) and 56 larvae (on $^{10}/_{4}$-39), while in the summer months the larvae seem to be rather rare. Off Helsingør the average number of larvae per main series was much larger. The maximum numbers per main series were here 2700 ($^{11}/_{11}$-41), 150 ($^{25}/_{10}$-41), and 140 ($^{19}/_{12}$-41 and $^{5}/_{9}$-42). It would seem that a small spawning sets in in the early spring, decreasing towards the summer, and followed by a new, much larger spawning in the autumn, which decreases towards January-February.

Other larvae of *Ascoglossa.* Besides the larva of *Limapontia* another larva is also abundant in the plankton from the Sound which as to the shape of the larval shell (fig. 157 A—G) shows such a close agreement with that of *Limapontia* (fig. 156 I—L) that it must be referred to the *Ascoglossa.*

The larva in question (fig. 157) has a sinistral, colourless, transparent and nearly globular shell with a narrow mouth. The columella has a very characteristic tooth, and the "suture", which forms a very elegant regular spiral, is broad and distinct. The spiral whorls indicated on the surface by the suture are only imaginary, as the shell inside forms only one large room without any whorls apart from that formed around the columella. This is clearly seen from fig. 157 B, where the retractor of the foot runs across the inner part of the shell. The liver is yellowish-brown, with large granules, the animal has two black eyes, but is otherwise quite colourless and transparent, with a rather small bilobed velum and a very large foot with an operculum. In older larvae the largest diameter of the shell is 340—365 μ.

Larvae taken in plankton off Ven on $^{25}/_{7}$-40 and placed in glass vessels were re-examined on $^{7}/_{8}$-40 (fig. 157 C-D). The greenish liver and the stomach had been withdrawn from the hindmost part of the shell; the retractor of the foot was not seen. The foot had increased considerably in size, and a propodium had formed. The velar lobes were nearly entirely reduced, and only a few cilia were still found along their margins. The eyes were somewhat larger, the statocysts distinct, and the operculum still intact. Fig. 157 E shows a larva, which — with the operculum intact — has left its larval shell. The velum is much reduced, but the shape of the liver and stomach seems to point to an abnormal development. On $^{10}/_{8}$-40 a couple of larvae were taken from fresh plankton and placed in a glass vessel for the night. Next morning a young animal was seen which was quite similar to that shown in fig. 157 E, and which, after having left its shell, swam readily backwards by the aid of the reduced velar lobes. Another specimen was studied while it was leaving its shell; in this case the operculum was discarded before the shell.

The facts given above show that the larva leaves its larval shell on metamorphosis. Further, considerable growth takes place during the pelagic life in contrast to the conditions in "true Nudibranchs", and this together with the shape of the shell point to the larva of an Ascoglossid. In addition to *Limapontia* only two species of Ascoglossids are known from the Sound, viz. *Elysia viridis* and *Stiliger bellulus.* Vogt (1846, as *Actaeon viridis*), and Pelseneer (1911, pl. 22, fig. 2) have figured the hatching larva of *Elysia viridis*, but these larval stages are so much younger than those sketched from the Sound that nothing can be said about their identity. An egg cord laid by a specimen of *Elysia viridis* during my stay at Gamborg Fjord (at the Little Belt) in July 1944 (Fig. 158 A-D) could not unfortunately be followed later than to the four-cell stage. However, the larva shown in Pelseneer's drawing does not differ so much from the older larvae in the Sound that they may not belong to one and the same species, so it is quite possible that our larva should be referred to *Elysia.* As far as I know, no figure of the veliger of *Stiliger bellulus* is given in the literature, but just hatched veligers of the related forms *Stiliger niger* (Lemche 1935) and *Stiliger gopalai* (Rao 1937) are described. The larva of the last-mentioned species has a large, black excretory organ very much like that of the *Philine* larvae, and seems thus to differ more from our larvae in the Sound than the larva of *Elysia viridis.* An undoubted identification cannot, however, be given at present.

The exact dates of occurrence of the larvae in the Ven plankton cannot be stated, because up to 1940 the larvae have been confused with other forms, but it is a fact that they are abundant in July, August, September, and October. From Helsingør exact observations are at hand. Larvae are here known from plankton taken on: $^{17}/_{9}$-41 (6 spms.); $^{7}/_{10}$-41 (4

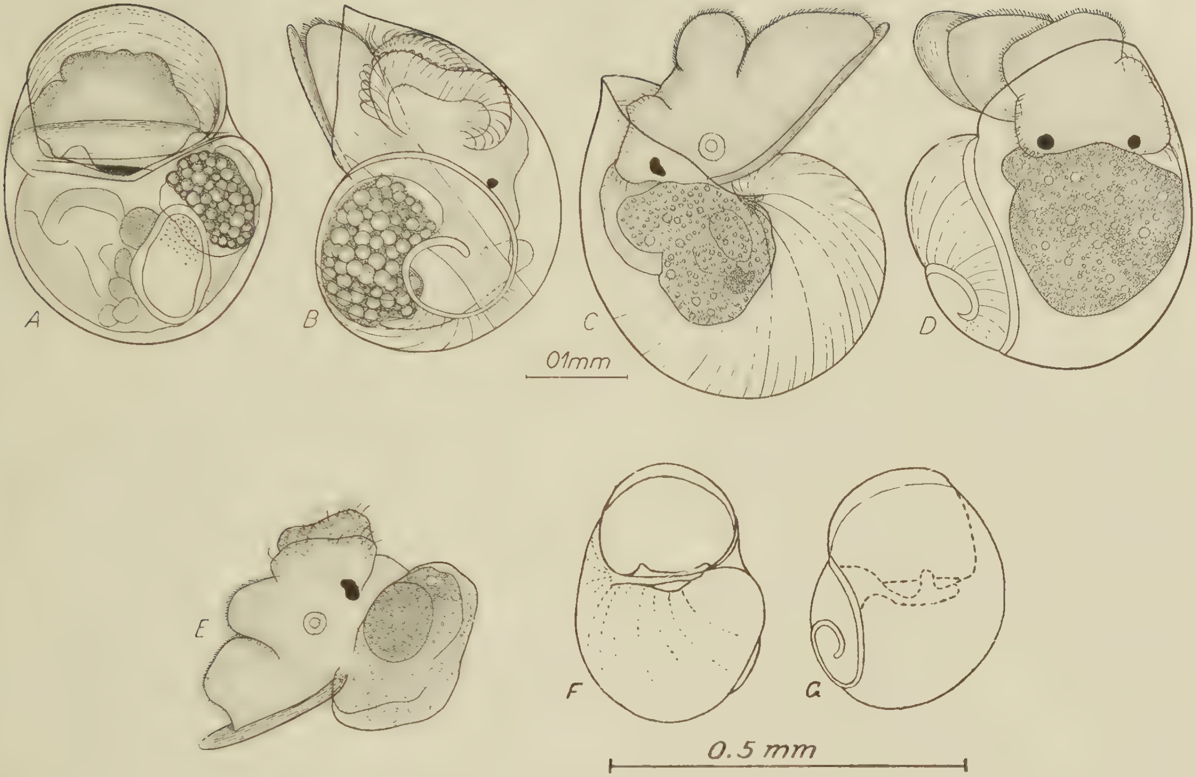


Fig. 157 A-G. Larvae belonging to an Ascoglossid sp., presumably to *Elysia viridis*. — *A* and *B*. Medium sized larva from plankton off Ven, depth 18-0 m, caught and drawn from life on $^{25}/_{7}$-1940. Seen from the ventral side (A) and the left side (B). — *C* and *D*. The same larva after having been kept in an aquarium to $^{7}/_{8}$-1940. The shell has increased in size, the velum is in dissolution, the foot has grown considerably, and the body has left the hindmost part of the shell. Seen from the right side (C), and from the dorso-lateral side (D). — *E*. The same larva a few hours later after having thrown off its shell. The larva is no doubt anomalous, but still the observations show that the larva will cast off its shell when metamorphosing. — *F* and *G*. The empty larval shell, seen from the ventral side (F), and the dorsal side (G).

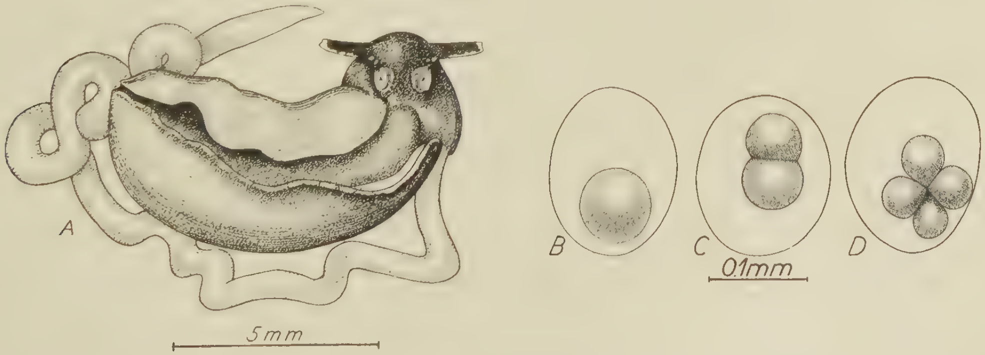


Fig. 158 A-D. *Elysia viridis*. — *A*. Adult animal in the act of spawning. Gamborg Fjord (at the Little Belt) on $^{14}/_{7}$-1944, drawn from life. The animal in question deposited the egg cord on *Fucus*. The whole spawning took about $1^{1}/_{2}$ hours, and the egg cord spawned contained about 7800 eggs. — *B* to *D*. Eggs in the first three cleaving stages from the egg cord fig. A.

spms.); $^{25}/_{10}$-41 (8 spms.); $^{4}/_{6}$-42 (1 large spm.); $^{21}/_{6}$-42 (7 large and medium-sized spms.); $^{6}/_{7}$-42 (1 spm.); $^{18}/_{7}$-42 (9 spms. in all stages of development); $^{25}/_{7}$-42 (94 spms. in all stages); $^{17}/_{8}$-42 (7 spms.), and $^{5}/_{9}$-42 (4 spms.). The main season is thus the summer and early autumn.

C. Nudibranchia.

In our investigation the Nudibranchs have only been dealt with rather summarily. The recognition of the larvae within this group in the Danish plankton requires a special technique and much time, which up to the present day have not been at our disposal. The planktonic larvae of the different genera and species are often so similar that only exact measurements and drawings of nearly each single larva found can decide its identity. It has therefore been necessary to leave the detailed treatment of this group to a special investigation. Mr. Erik Rasmussen has started such an investigation and has already cleared up the breeding biology and the larval development in a couple of forms from Danish waters. His results will be published later and will thus form a valuable supplement to the remarks given here.

Twenty-seven species of Nudibranchs (apart from the Ascoglossids) are at present known from the Sound in the adult stage, viz. *Duvaucelia plebeja*, *D. hombergi*, *Polycera quadrilineata*, *Goniodoris nodosa*, *Onchidoris proxima*, *O. muricata*, *O. diaphana*, *Idalia elegans*, *Acanthodoris pilosa*, *Cadlina obvelata* (= *repanda*), *Rostanga coccinea*, *Archidoris tuberculata*, **Jorunna tomentosa*, **Idulia coronata* (off Hellebæk), *Pleurophyllidia loveni*, *Dendronotus arborescens*, **D. robustus* (off Helsingør), *Coryphella rufibranchialis*, *C. gracilis*, *Eubranchus pallidus*, *E. viridulus*, *Hero formosa*, *Embletonia pallida*, *Hervia modesta*, *Favorinus branchialis*, *Aeolidia papillosa*, and *Facelina drummondi*. The three species marked with an asterisk have not hitherto been published from the Sound; these finds have kindly been placed at my disposal by Mr. Per-Magnus Lovén (Malmö Museum) and Mr. Erik Rasmussen.

As already mentioned, 69 species of Prosobranchs are known from the Sound, and it is a fact that the larvae of these Prosobranchs play a very important part in the plankton. As the number of Nudibranch species constitutes 39 per cent of that of the adult species of Prosobranchs, it seems likely at the outset that the Nudibranch larvae are of a fairly great importance in the Sound plankton also. This, however, is not the case. Off Ven the Nudibranch larvae in the plankton constitute 3 per cent and off Helsingor only 11 per cent of the number of Prosobranch larvae. Hence, it seems necessary to examine the different types of Nudibranch larvae and their "fitness" for a pelagic life.

Vestergaard & Thorson (1938) distinguish between three types of larval shells within the northern Nudibranchs, viz.:

Type A. Simple cup-shaped shells without any trace of whorls.
Type B. Spiral shells, normally forming $^{3}/_{4}$ to 1 whorl only.
Type C. Egg-shaped "inflated" shells (fig. 159, 160 A-C). (This type of shell is also known for the Tectibranch *Acera bullata*, fig. 148 B-E.)

The next step is to find out the distribution of these three types over the individual groups of Nudibranchs. While the spawn is known and described for a very large number of Nudibranchs within northern seas also, only some few of the authors which deal with the biology of the Nudibranchs have observed the development of the embryos and described the hatching larvae. Standard works, in which such northern larvae are sketched, are those of ALDER & HANCOCK (1845—1855), TRINCHESE (1881), MAZZARELLI (1906), and PELSENEER (1911). In addition VESTERGAARD & THORSON (1938) and RASMUSSEN (1944) have described the larvae of a few Danish species; ALYSON BEHRENTZ (1931) has described the larva of *Onchidoris muricata* from Norway. Although most of the sketches of larvae in the literature show so few details that they cannot be used for a direct identification of the larvae in the plankton, the sketches are sufficiently detailed to show the type of larval shell for each species examined. From the available literature I have been able to gather information about the type of the larval shell in 24 species of northern Nudibranchs. The results are given in the list below:

Duvauceliidae: Larval shell of type A, known for:
  ***Duvaucelia plebeja.* — (VESTERGAARD & THORSON 1938).
Polyceridae: Larval shell of type B, known for:
  ***Polycera quadrilineata.* — (ALDER & HANCOCK 1845—55, MAZZARELLI 1906).
  **Palio (Polycera) lessoni (= ocellata).* — (MEYER & MÖBIUS 1865).
  **Ancula cristata.* — (PELSENEER 1911).
  ***Goniodoris nodosa.* — (PELSENEER 1911).
  **Onchidoris bilamellata.* — (PELSENEER 1911).
  ***Onchidoris muricata.* — (ALYSON BEHRENTZ 1931).
  ***Acanthodoris pilosa.* — (PELSENEER 1911).
Dorididae: Larval shell of type B, known for:
  ***Archidoris tuberculata.* — (ALDER & HANCOCK 1845—55).
Iduliidae: Larval shell of type B, known for:
  ***Idulia (Doto) coronata.* — (ALDER & HANCOCK 1845—55, MAZZARELLI 1906, TRINCHESE 1881).
  Antiopa (Janus) cristata. — (TRINCHESE 1881).
Dendronotidae: Larval shell of type C, known for:
  ***Dendronotus arborescens.* — (ALDER & HANCOCK 1845—55, PELSENEER 1911).
Flabellinidae: Larval shell of type C, known for:
  ***Coryphella rufibranchialis.* — (THORSON, unpublished sketches from East-Greenland).
  Eubranchus (Galvina) pictus. — (TRINCHESE 1881).
  ***Eubranchus pallidus.* — (VESTERGAARD & THORSON 1938, RASMUSSEN 1944).
  Amphorina coerulea. — (TRINCHESE 1881).
Tergipedidae: Larval shell of type C, known for:
  ***Embletonia pallida.* — (ALDER & HANCOCK 1845—55, RASMUSSEN 1944).
  Tergipes despectus. — (PELSENEER 1911).
  Amphorina olivacea. — (PELSENEER 1911).
  Cratena concinna. — (PELSENEER 1911).
Aeolididae: Larval shell of type B, known for:
  ***Favorinus branchialis.* — (Verbal information supplied by ERIK RASMUSSEN).
  **Facelina coronata.* — (ALDER & HANCOCK 1845—55).
  ***Aeolidia papillosa.* — (PELSENEER 1911).

Thirteen of these species (marked with two asterisks) are known as adults from the Sound itself, and four further species (marked with one asterisk) are known from the adjacent waters, viz. the Kattegat and the Baltic. — The facts given above are fairly interesting, and show that the cup-shaped, simple larval shell is rather rare, while the other two types —

apparently equally frequent — are restricted to special families, viz. the spiral-shelled larvae with $^3/_4$ to 1 whorl (type B) to the *Polyceridae, Doridae, Iduliidae,* and *Aeolididae*, and the egg-shaped, inflated larval shells (type C) to the *Dendronotidae, Flabellinidae,* and *Tergipedidae*.

If we compare the three larval types mentioned above with those of the pelagic larvae of the Prosobranchs, it will easily be seen that the Nudibranch larvae are rather unfit for a long pelagic larval life. The types of shell, the small velum, and the lack of eyes in the Nudibranch larvae are characters which, on the contrary, are suggestive of a shortened pelagic life. In agreement with this, it is also a fact that the shell of the pelagic Nudibranch larvae is of nearly the same size during their whole planktonic life. If a growth in size takes place, this will be quite inconsiderable. The planktonic stage of the Nudibranchs is of importance for the distribution of the species, but is of little or no value as a feeding stage, in contrast to the conditions found in the larval Tectibranchs and Ascoglossids, which grow and feed readily in the plankton. The three types of northern Nudibranch larvae are also more or less fit for a planktonic life. As is known from the Prosobranchs, larvae which are especially adapted to a long pelagic life are provided with an extra larval shell, viz. the *Echinospira* shell, which is much more inflated than the simple larval shell and by its larger displacement seems to hold the larva afloat in the water. While in the Nudibranchs the larval shells of types A and B are small and narrow, the egg-shaped inflated shells of type C are of a much larger displacement and seem to be much more fitted for a pelagic life. — Larvae of *Eubranchus pallidus* hatched in aquaria are able to swim about for several weeks — a fact which may be due to the special aquarial conditions or to the lack of a suitable substratum (cf. pp. 463—465). In *Embletonia pallida*, which has also egg-shaped inflated larval shells, Rasmussen (1944), however, found that the larvae may drop the larval shell before leaving the spawn, i. e. the larvae may have no pelagic stage at all. Fig. 159 shows a larval Nudibranch of type C, which, though it has no lines of growth on its shell, is in the crawling stage and has a reduced velum with only a few cilia left. A stage like this will hardly spend any long time in the plankton.

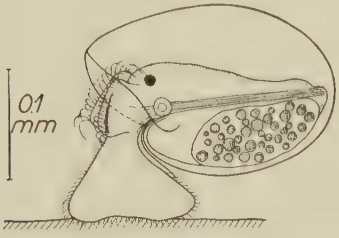


Fig. 159. Nudibranch-larva of type C (see the text p. 270) in the stage of metamorphosis (swimming-crawling stage). From plankton off Ven, depth 18-0 m, on $^{25}/_7$-1940 (drawn from life the same day). The animal crawled on the bottom of the glass dish and was able to rise the shell to a vertical position. The velum is already much reduced, no connection exists between the retractor-muscle and the hindmost part of the shell, and the foot has grown to a large size. The shell shows not the slightest sign of growth during the larval life.

The conclusions of the above reflectations are, then, that Nudibranch larvae of types A and B are very poorly equipped for a planktonic life. If they are at all planktonic, their stay in the plankton must be assumed to be very short (probably a few hours to a few days). Larvae of type C are better adapted for the pelagic life, but the small velum, the slow growth, etc., seem to show that these larvae also stay for a rather short time in the plankton (cf. p. 436).

The results arrived at above are in good agreement with the data supplied by plankton samples. Larvae of types A and B were not observed in our main series. It is not, of course, impossible that occasional specimens may now and then have been overlooked or confused with very young larvae of Prosobranchs, but even in that case they must have been very rare and of no importance at all in the plankton. Larvae of type C, however, are present in the plankton in all the months of the year. On an average 17 of these larvae per main series have been found off Ven (577 larvae of Prosobranchs) and 81 off Helsingor (728 larvae of Prosobranchs). The maximum occurrence is found in the months October to January (e. g. off Ven per main series 72 spms. on $^5/_1$-38 and off Helsingør 470 spms. on $^{11}/_{11}$-41, 246 spms. on $^{25}/_{10}$-41, 130 spms. on $^{19}/_{12}$-41, and 130 spms. on $^{31}/_1$-42). Further, from late December to the middle of April larvae of type C are often the dominating Gastropod larvae in the plankton, but this is not due to their large number but to the nearly total absence of Prosobranch larvae in these months.

As already mentioned, we had no opportunity to identify the Nudibranch larvae in our plankton. Several of them were not sketched at all, but still we were able throughout the year to distinguish at least six different larvae of type C which were regularly met with in the plankton, viz.

1. Small, quite transparent larvae, 225 μ in largest diameter of the shell, without pigmentation and without any granulation in the liver. They agree fairly well with the sketches in ALDER & HANCOCK (1845—55) of *Dendronotus arborescens* and should probably be referred to this species. Occurrence: June to September (occasionally November, December, and January).
2. Larvae, quite similar to those described above, but twice as large (no figures). Occurrence: April to September (December).

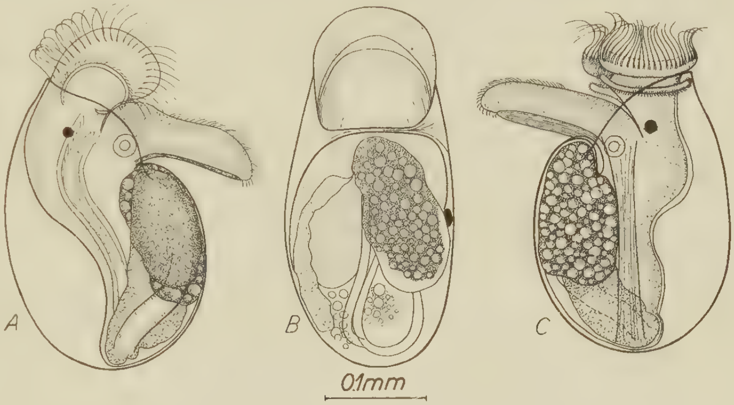


Fig. 160 A-C. Larvae of Nudibranch sp. of the type mentioned on p. 271, No. 5. From plankton off Ven, depth 18-0 m, caught and drawn from life on $^{25}/_7$-1940 (fig. A and C), and on $^1/_8$-1940 (fig. B). Seen from the right side (A), the ventral side (B), and the left side (C).

3. Transparent colourless larvae with an egg-shaped shell about 200 μ in largest diameter and with a wider mouth than in the preceding species (no figures). Occurrence: May to June.
4. Rather opaque larvae, largest diameter of the shell 230 -235 μ, with a slight granulation and with small grains of carmine pigment in the body wall. According to ERIK RASMUSSEN (verbal information) this larva seems to belong to *Eubranchus pallidus*, which is more opaque in the older larvae, and accordingly the animal (not the shell) has grown and taken in food during its planktonic life. This larva is by far the commonest larval Nudibranch in the plankton. It may be found throughout the year, but the main season is from December to May, when up to 130 specimens have been found in a single main series ($^{31}/_1$-42, off Helsingør).
5. Opaque, granulated larvae, largest diameter of the shell 265 μ, resembling larvae of the Tectibranch *Acera bullata* (cf. fig. 148 B-E, p. 253) but somewhat smaller (fig. 160 A-C). Occurrence: June to September, and in addition abundant in December.
6. Larvae of the normal egg-shaped inflated type but with a tendency to a spiral suture on the left side of the shell. Animal rather opaque (no measurements, no figures).

Of the 27 species of adult Nudibranchs known from the Sound, nine species seem to belong to a systematic group in which larvae of "type C" may be met with. Thus it might be expected that two further species of larvae of "type C" would be found in the plankton from the Sound, while those of *Eubranchus pallidus* are non-pelagic.

General Discussion of the Opisthobranchs.

At present the bottom stages of 41 species of Opisthobranchs are known from the Sound viz. 11 Tectibranchs, 3 Ascoglossids, and 27 Nudibranchs. As mentioned on p. 245, only the Tectibranchs and the Ascoglossids have been dealt with in detail, while the Nudibranchs will be treated in a later special report by Mr. Erik Rasmussen.

The present investigation has revealed a fundamental difference in the "ecological type" of the larval development in Tectibranchs and Ascoglossids as compared with that of the Nudibranchs. The Tectibranch larvae grow and feed vigorously during their pelagic life, and so do the Ascoglossids, which is the more remarkable, since this group has hitherto been regarded as belonging to the Nudibranchs. The discussion of the systematic position of the Ascoglossids and the tendency during recent years to refer them to the Tectibranchs is strongly supported by the type of their larvae. The Nudibranchs, however, have a much shorter pelagic stage, which seems to be quite, or nearly, independent of the plankton as a source of food. This latter conjecture is supported by the fact that larval Nudibranchs normally occur in rather considerable numbers in the plankton during the winter season, when the Prosobranch larvae are absent and no production of phytoplankton takes place in the Sound. Apart from *Embletonia pallida*, however, all other Danish Nudibranchs hitherto examined seem to hatch in the veliger stage, and are thus able to swim about. For two of the types of Nudibranch larvae, viz. types A and B (cf. pp. 268—269), the pelagic life must be supposed to be extremely short. They play no part at all in the plankton, while the third type—type C (cf. pp. 268—269)—with its egg-shaped inflated shells was met with regularly in our main series. However, also this latter type shows no or only a slow growth in the plankton and seems only to feed on the plankton to a small extent, or not at all. Thus these egg-shaped larvae should most probably be referred to the lecithotrophic pelagic type (cf. pp. 436—438), the planktonic life of which is a spreading stage and not a feeding stage.

As regards the 14 Tectibranchs and Ascoglossids, which will here be discussed together, the type of larval development is known and the larvae have been identified for 10 species, i. e. $71^1/_2$ per cent, which all have a long planktotrophic pelagic life, viz. *Actaeon tornatilis*, *Retusa truncatula*, *R. umbilicata*, *Diaphana hyalina*, *Acera bullata*, *Philine aperta*, *P. scabra*, *P. quadrata*?, *P. punctata*, and *Limapontia capitata*. The larvae of all these species, apart from those of *Philine punctata*, have been found in the Danish plankton and identified. As to the four remaining species of the fourteen known from the Sound, the apex-studies of Dr. Lemche have shown that *Retusa obtusa* (= *pertenuis*) has a non-pelagic development, which is in good agreement with its dominance in high-Arctic seas. The larval development of *Tylodina duebeni* is totally unknown. *Elysia viridis* is known to have pelagic larvae, but the duration of its pelagic life is unknown; the "unidentified larval Ascoglossid" present in our plankton is probably the larva of *Elysia*. Finally, *Stiliger bellulus* is unknown as to reproduction and larval type, but other species of *Stiliger* are known to have a pelagic stage (duration unknown). Thus we know the larval development of 12 of the 14 species from the Sound, i. e. 86 per cent, and 11 of these 12 species, i. e. 92 per cent, seem to have a long pelagic life.

Adult Tectibranchs constitute no large percentage of the bottom fauna in the Sound. In 300 bottom samples (Petersen 1911, table VI, no. III—VIII) taken throughout the Sound, the number of adult Tectibranchs seems to constitute about 1 per cent only of the number of adult invertebrate specimens on the level sea bottom, and a rough calculation seems to show that they constitute about 0.5 per cent if the epifauna is also included. If the Ascoglossids are referred to this group, the total percentage will increase somewhat, but will not exceed 1 per cent of all the invertebrate specimens living on the bottom of the Sound. — Similarly the larvae of Tectibranchs and Ascoglossids constitute 3 per cent of all the bottom animal larvae in the plankton (viz. Tectibranchs 1.7 per cent, Ascoglossids 1.3 per cent), that is to say off Ven 2 per cent (Tectibranchs 1.8 per cent, Ascoglossids 0.2 per cent) and off Helsingør 4.1 per cent (Tectibranchs 1.6 per cent, Ascoglossids 2.5 per cent) — figures which agree fairly well with those found for the bottom stages.

Fig. 193 on p. 374 and fig. 194 on p. 377 show the occurrence of Tectibranch and Ascoglossid larvae in our main series off Ven and off Helsingør respectively. The table on p. 372 is a supplement to the figures from Ven, and comprises the main series in the months from August 1936 to August 1937, from which only an estimate, but no exact counts, are at hand. — Off Ven (fig. 193) the season of occurrence seems to be April-May to October with a maximum in July and August, while larvae are nearly absent in the period November to April. — Off Helsingør the season of occurrence is April to December with a maximum in July to September, and a sudden extra maximum in November — the latter is almost exclusively due to the abundance of larvae of *Limapontia capitata*. As a general rule it can be stated that the Tectibranchs are most frequent during the summer and autumn, while the Ascoglossids, especially *Limapontia*, dominate in the spring and the late autumn.

The pelagic Tectibranch larvae examined in our main series during the three years' exact counts, viz. from Ven 3136 (45 main series) and from Helsingør 2389 (20 main series), totalling 5525 larvae, show the following percentage distribution:

	Off Ven	Off Helsingør	Total
Actaeon tornatilis	0.0 %	0.2 %	0.1 %
Retusa umbilicata	24.7 -	12.4 -	19.4 -
Diaphana hyalina	3.3 -	2.4 -	2.9 -
Acera bullata	25.6 -	13.5 -	20.4 -
Philine aperta	32.9 -	67.2 -	47.7 -
Philine scabra	1.6 -	1.2 -	1.4 -
Philine ?quadrata	0.5 -	0.0 -	0.3 -
Philine sp. (small ones)	11.3 -	3.1 -	7.8 -
Unknown species	0.1 -	0.0 -	0.0 -
	100.0 %	100.0 %	100.0 %

Dominants are, thus, *Philine aperta*, with more than twice the frequency of any other species, *Acera bullata*, and *Retusa umbilicata*, these three species constituting together 87.5 per cent of all the Tectibranch larvae in the Sound. If some of the young larvae of "*Philine sp.*" should be referred to *Philine aperta*, which is most likely, the percentage will be still higher. It is surprising that the larvae of *Diaphana hyalina* and *Philine scabra* is of such little importance in the plankton, since the bottom stages, especially of the latter species, seem to be rather common in the Sound.

The corresponding percentages for the pelagic Ascoglossid larvae from the same period, viz. from Ven 393 (45 main series) and from Helsingør 3751 (20 main series), totalling 4144 larvae, show the following percentage distribution:

	Off Ven	Off Helsingør	Total
Limapontia capitata	75.8 %	94.3 %	92.5 %
?Elysia viridis	24.2 -	5.7 -	7.5 -
	100.0 %	100.0 %	100.0 %

Thus *Limapontia* is absolutely dominant here, and it is interesting to note that the actual number of *Limapontia* larvae in the Sound (3838 larvae in all the main series from Ven and Helsingor) far surpasses the number of larvae of *Philine aperta* (2638 larvae in all the main series), which is regarded as the only species of any quantitative importance in the bottom stage.

Among the larvae of the groups *Tectibranchiata* and *Ascoglossa* it is very easy to distinguish roughly between those derived from infauna parents and epifauna parents respectively. The Tectibranchs are almost exclusively associated with the level bottom, while the Ascoglossids live in the vegetation. If, therefore, the Tectibranchs and the Ascoglossid larvae together are estimated at 100 per cent, the distribution of these groups over the infauna and the epifauna will show the following figures:

Ven plankton		Helsingør plankton		Average for both stations	
Infauna = Tectibranchs	Epifauna = Ascoglossids	Infauna = Tectibranchs	Epifauna = Ascoglossids	Infauna = Tectibranchs	Epifauna = Ascoglossids
3136 larvae = 88.8 %	393 larvae = 11.2 %	2389 larvae = 38.9 %	3751 larvae = 61.1 %	5525 larvae = 57.1 %	4144 larvae = 42.9 %

The epifauna larvae seem, thus, to be somewhat less frequent than the infauna larvae. It will be seen that the infauna larvae dominate markedly in the two years' main series taken off Ven, while the epifauna larvae were predominant off Helsingor (1 year's main series only); this is especially due to the sudden maximum of *Limapontia* larvae which occurred in November 1941. Hence, it seems most likely that the percentage of Tectibranch larvae for a longer series of years will be still larger than shown by the above figures. The swarms of Tectibranch larvae are distributed over several different species, three of which are at least rather numerous, while the swarms of Ascoglossid larvae are totally dominated by the presence or absence of *Limapontia capitata*, which, as shown from the three years' main series, may fluctuate enormously from year to year. Also from the year August 1936 to August 1937 the *Limapontia* larvae taken off Ven seem to be much fewer in number than off Helsingør in 1941.

While the Prosobranchs show several different modes of spawning and development of their eggs (cf. p. 240), all the northern Tectibranchs and Ascoglossids examined seem to shed their eggs in a gelatinous layer of different type and shape, from which the larvae will not hatch until the veliger stage, i. e. until they are able to feed on the plankton. The young veligers of these groups found in the Sound plankton may accordingly be supposed to originate from parents living in the Sound itself or the adjacent areas. The rather large number of larval specimens of these groups as compared with the calculated number of specimens in the bottom stage seem also to support this fact.

The duration of the pelagic larval life is unknown for all the species of Tectibranchs and Ascoglossids, at any rate in the northern seas. The power of resistance of these larvae to changes in the salinity and temperature seems, however, to be rather great. Especially the larvae of *Limapontia capitata* seem to be capable of enduring great variations. As was the case with the larval Prosobranchs (see p. 244), the shell and operculum of the Tectibranch and Ascoglossid larvae seem also to provide a good protection against sudden variations in the salinity.

The larvae of these two groups seem to feed exclusively on phytoplankton. — They may further be supposed to be devoured by other animals in a similar degree as the Prosobranch larvae (which see), but nothing definite can be stated.

Of the 27 species of Nudibranchs known from the Sound, 2 belong to "type A" with a cup-shaped shell without whorls, 16 belong to "type B" with simple spiral shells of $^3/_4$ to 1 whorl only, and 9 belong to "type C" with egg-shaped inflated shells. Larva of types A and B play no important part in the plankton, and their larval life — though pelagic — must be regarded as extremely short. Larvae of "type C" were regularly met with in our plankton samples — a fact which seems to show that they have a pelagic life of at least a few days, during which they seem to take no or only little food from the plankton. Thus, their larval shell seems hardly to grow during their planktonic life, and most likely they may be referred to the lecithotrophic larvae (cf. pp. 436—438).

Larvae of this type, probably found in nine species in the Sound, may, however, be reduced to eight species of pelagic larvae, because *Embletonia pallida*, according to RASMUSSEN (1944), has a non-pelagic development. Of these eight larval species, which must be supposed to have egg-shaped, inflated, pelagic larval shells, we were able to distinguish at least six species of larvae in our main series (cf. p. 271).

Nudibranchs in the bottom stage seem to play a rather small part in the Sound. They are quite absent from the level sea bottom, and their occurrence in the epifauna can only be roughly estimated, but it seems to be of little importance. In the Sound they hardly constitute more than 1 to $1^1/_2$ per cent of all the invertebrate specimens in the bottom stage which reproduce by pelagic larvae. Similarly, the larvae off Nudibranchs constitute 0.7 per cent of all the bottom animal larvae in the plankton, thus off Ven 0.4 per cent and off Helsingør 1.1 per cent.

Fig. 193 on p. 375 and fig. 194 on p. 377 show the occurrence of Nudibranchs in our main series taken off Ven (see also the table on p. 372) and Helsingør. — Off Ven (fig. 193, "other Invertebrate larvae") larvae were met with all the year round, but the largest numbers of larvae seem to occur from early January to April-May. — Off Helsingør (fig. 194) the most constant occurrence seems to be from December to May, with a sudden large maximum in October-November (corresponding to the maximum here of *Limapontia capitata*). Off Helsingør larvae were likewise found throughout the year.

All the larvae of this group are derived from epifauna parents. They are spawned in gelatinous bands or envelopes, and hatch in the veliger stage. Their resistance to changes in the salinity and temperature seems to be just as great as among the Tectibranchs, Ascoglossids, and Prosobranchs. The duration of their pelagic life is usually very short, or rather short, under natural conditions. On certain occasions, however, it may be considerably prolonged. Thus, under unfavourable conditions in aquaria larval Nudibranchs may swim about for one or two months.

Nudibranch larvae will normally take no — or only little — food from the plankton. Larvae of *Archidoris tuberculata*, however, are known to be able to feed on small phytoplankton organisms of the species *Pleurococcus unicornis* (ALLEN & NELSON 1911).

Summary of Discussion.

Forty-one species of Opisthobranchs are known from the Sound as adults, larvae, or both, viz. 11 Tectibranchs, 3 Ascoglossids, and 27 Nudibranchs. While the Tectibranchs and Ascoglossids feed and grow vigorously in the plankton, the Nudibranchs have an extremely short or a rather short pelagic life, during which their shells do not increase in size and they take no or only little food from the plankton. — Of the 14 species of Tectibranchs and Ascoglossids, the type of larval development is known for 12, i. e. 86 per cent. Eleven of these 12 species — 92 per cent — have a long pelagic life.

In the bottom stage Tectibranchs and Ascoglossids constitute about 1 per cent of all the invertebrate specimens with pelagic larvae in the infauna, and about 0.5 per cent only if the epifauna, also, is included. The larvae of these groups represent about 3 per cent of all the invertebrate larvae found in the Sound plankton. The larvae normally hatch as fully developed veligers. Their power of resistance to changes in the salinity and temperature is fairly great, especially in *Limapontia capitata*. The larval seasons are as follows: Tectibranchs have their main occurrence in the plankton from April-May to October with a maximum in July-September; dominants: *Philine aperta, Acera bullata*, and *Retusa umbilicata*. Ascoglossids with *Limapontia* as dominants are commonest in the spring and late autumn; larvae are nearly absent in the months December to April. — The larvae of *Philine aperta* constitute 47.7 per cent, those of *Acera bullata* 20.4 per cent, and those of *Retusa umbilicata* 19.4 per cent — totalling 87.5 per cent — of all the Tectibranch larvae in the Sound, but the larvae of *Limapontia* are more numerous in the plankton than those of *Philine aperta*. When the larvae of Tectibranchs and Ascoglossids together are estimated at 100 per cent, 57.1 per cent of them will fall upon larvae with infauna parents (= all the Tectibranchs), while 42.9 per cent fall upon larvae with epifauna parents (= all the Ascoglossids). However, this estimate may be influenced from year to year by large fluctuations in the stock of *Limapontia* larvae.

Of the 27 species of Nudibranchs, 18 belong to larval types which — though veligers — have a very short planktonic stage. The nine species left have egg-shaped inflated shells; one of them is non-pelagic, while the others are supposed to have a pelagic stage of at least some few days. Such larvae, which were actually met with in our plankton, constitute only 0.7 per cent of all the bottom animal larvae here — a figure which agrees well with the number of the adults. — Nudibranch larvae occur in the plankton throughout the year, being most constant and numerous from December to May; they are all derived from epifauna parents.

9. Lamellibranchia.

by

C. Barker Jørgensen.

In the investigations on the reproduction and larval development of the Danish marine invertebrates which have been carried out by Dr. Gunnar Thorson and his assistants near Ven in the years 1937—39 and near Helsingør in 1941—42 the working up of the Lamellibranch larvae was entrusted to me[1]).

The investigations consisted in an identification of the pelagic Lamellibranch larvae of the Sound and in regular counts — made at intervals of about a fortnight — of the veligers in the plankton samples, which were taken under standard conditions. The plankton samples were secured in a number of hauls taken from the bottom to the surface with a plankton net of gauze No. 12. The diameter of the opening of the net was 25 cm. Up to May 10, 1938, each series consisted of ten such vertical hauls, later on, however, only of five hauls. The numbers of the larvae found in the five-haul samples have all been multiplied by two; thus all the numbers of Lamellibranch larvae found in a plankton sample as given in the following pages always have reference to the number of larvae found in ten vertical hauls, which will be termed a "main series". The numbers from Ven and Helsingør are not directly comparable, since near Ven the water column passed through by the net was c. 18 m while near Helsingør it was c. 30 m. (For details of the technique of the investigations, etc., the reader is referred to Dr. Thorson's paper p. 14).

In 1937, however, the conditions hardly allowed the counting of the pelagic larvae of the individual Lamellibranch species. Our knowledge of the veligers was then quite sporadic. In "Die Acephalen des nordischen Planktons" by Simroth (1913) only the veligers of *Ostrea edulis* and *Mytilus edulis* as well as the representatives of some few families are recorded from our waters. However, later works by Odhner, Kändler, Miyazaki, and other authors up to 1937 had increased this number by some further species and families. When our investigations began, only a small number of the types of veligers found in the plankton could be referred to their family or species. In treating the larvae which could not be determined on the basis of the available literature the procedure must, accordingly, be to refer the veligers to the different types, which were subsequently drawn and provided with provisional serial numbers until identification was possible.

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[1]) I wish to express my cordial thanks to Dr. Thorson for countless hours of valuable collaboration on Ven and at Helsingør. Cordial thanks are likewise due to mag. sc. Poul Bondesen, who undertook the treatment of the Lamellibranch larvae during my absence from the autumn of 1937 to the autumn of 1938.

An exhaustive assignment of a collection of unknown veligers to types each of which was to be identical with one and only one species, is difficult for several reasons, and during the first years of our investigations the assignment was not quite successful and even at present it is not yet quite practicable.

In the first place, our counts always comprised a group of "small indeterminable larvae", that is to say, chiefly young non-characteristic and indeterminable stages of the veligers otherwise present in our samples and referred to type; but in addition this group, at any rate during the first years of our investigations, included but little conspicuous small veligers less than c. 200—250 μ long, which metamorphosed at such small lengths.

However, it was also difficult to refer the larger veligers to type. Thus in some cases one of our registered types proved to comprise more than one species (cf. e. g. the Tellinides and Semelides on pp. 297—300), and conversely, in other cases several types had to be included under one species (cf. e. g. *Spisula subtruncata*, p. 301). The essential difficulty in the differentiation into types of the available material of larger Lamellibranch veligers found in the plankton was the delimitation of the species, since we did not know, and still often only somewhat imperfectly know, the range of variation of the individual species. The descriptions of larvae which were available in 1937, when we commenced our work, were as a rule given in such general terms that in most cases they could only be used for a determination of the species when the veligers presented such a remarkable shape of the shell that the identification could be made on the basis of the shell markings alone, and, at the same time, there were no possibilities of confusion. The same applies to the greater part of the literature on the Lamellibranch veligers from our waters which has been published later. Most authors in their descriptions have only taken those characters into consideration which can be directly observed on the living larva under the microscope, that is to say, the shape of the shell (including various absolute measurements and measurement indices), the colour and structure of the shell, and the shape and colour of the different internal organs. Many of these descriptions are directly misleading, however, because the concrete data were insufficient, but the variations have been greater than assumed, if not within the material on which the descriptions are based, at any rate within material derived from other localities, or from the same locality but collected at different times. This especially applies to the statements about the shape and colour of the shells and the colour of the soft parts. Many examples of this are given below.

The only paper dealing with the European waters in which a more comprehensive characterisation of a number of pelagic Lamellibranch larvae has been attempted is that of Werner (1939). In addition to the characteristics of habit which can be directly observed on the living larva, he has given special attention to the description of the hinges and to the size and shape of prod. I[1]).

In the cases in which even the veliger exhibits differentiation of the hinges, this is one of the most important larval characters, though its full systematical value cannot be fixed until a larger material for comparison than that now in our possession is available. However, that the veliger hinge alone is insufficient for a determination of the species in many cases — perhaps in all cases — is evident even at the present time. In the first place, many species have no differentiation of the hinge until after metamorphosis, and secondly it has turned out that in species of the same family, and even of different families which possess a larval or rudimentary final hinge during their planktonic life, the hinges may be quite identical. This is, for instance, the case in several species of *Pecten* and in *Macoma, Tellina,* and several others. It is probably the general rule that species within the same family have at first identical, or very nearly identical, hinges.

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[1]) Prod. I = prodissoconch I, i. e. the part of the larval shell first developed differing in structure from the remainder of the prodissoconch (cf. Werner 1939).

The length and shape of prod. I will no doubt be of great importance to future larval systematics, even though our experiences as regards the reliability of the length of prod. I as a specific criterion is not as promising as supposed by WERNER. WERNER states that prod. I varies but slightly in the species examined by him, but he says nothing about the range of the variation. This is in opposition to the exceedingly great variations in the length of prod. I that was sometimes found by us. And the prod. I lengths measured by us in the same species as were examined by WERNER in no case agree with the lengths given by him (see e. g. *Mytilus edulis, Macoma baltica, Cultellus pellucidus* and *Zirphæa crispata,* which constitute the four species that were treated by WERNER. Cf. also the remarks under *Teredo navalis*). It is difficult to give an opinion as to the reason for this discrepancy, especially since we do not know the factors which are decisive for the size attained by prod. I. It seems, however, not to be the egg-size alone which determines the size of prod. I, as the divergencies in the size of prod. I seem to be comparatively larger than in the egg size. However, the question requires a more careful examination.

The maximum size of the veliger at metamorphosis has often been used in the characterisation of the veliger larva, in a single case it has even been used as a character in a key of determination—the only one available—of Cardides in the Channel (LEBOUR 1938 a). However, this character, also, is of less absolute value than has been ascribed to it by most authors. In our waters, at any rate, the maximum veliger size in a large number of cases (e. g. in *Mytilus edulis, Cardium edule, Mya arenaria,* etc.) varied much more than stated in the literature. There seems to be a greater or smaller correlation between the size during metamorphosis and the environment, though at present it is impossible to give any exact particulars.

Since our investigations commenced, we have succeeded in determining the species of the greater number of the veliger types which were met with in the plankton of the Sound. The identification was carried out chiefly by the aid of bottle collectors (see THORSON p. 19—23), rearing in aquaria, and comparisons between the veligers and the prodissoconchs of young bottom stages, i. a. from the collections of the Zoological Museum, Copenhagen, though as to a number of species we have drawn on the works by LEBOUR and WERNER published in 1938—39. Of the c. 45 species whose larvae may be assumed to be fairly frequently met with in the plankton of the Sound, c. 28 were identified with a greater or smaller amount of certainty, while c. 5 hide among the registered, but not identified, larval types. However, none of these were of frequent occurrence.

The distribution of the larvae over species and number during the year from September 1941 to September 1942 is shown in the subjoined table (p. 311). The previous years show a similar, but less specified larval distribution than the table, even though the individual species may vary somewhat as regards the dates for their first and last occurrence in the plankton, as will appear from the particulars given below under the individual species. The figures stated have reference to the contents of a main series consisting of ten vertical hauls (cf. p. 14). The meaning of the individual symbols is as follows: × = 1—19, ×× = 20—199, ××× = 200—999, ×××× = 1000—1999, and ××××× = more than 2000 individuals. The size of the group "small indeterminable larvae" varies rather independently of the total number of veligers in a main series, but is comparatively small when the number of species is small. This is due to the fact that the species of the individual veligers can in most cases be determined at a much smaller absolute size when only very few species are represented in the plankton, as is for instance the case in the spring, than is possible at other times of the year. The small "indeterminable larvae" should generally be distributed fairly proportionally over the remaining larval types occurring at the same time.

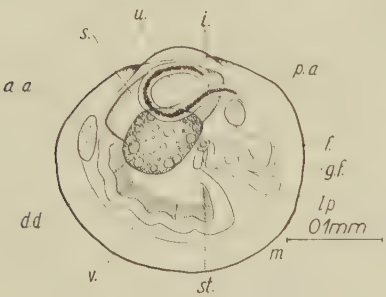

Fig. 161. Type of a Lamellibranch-veliger (*Spisula subtruncata*, see p. 301) a. a. anterior adductor, p. a. posterior adductor, u. umbo, m. mantle, v. velum, f. foot, l. p. labial palp, s. stomach, d. d. digestive diverticulum, i. intestine, st. statocyst, g. f. gill filaments.

When in the following pages the number of veligers of a certain species is given as the number of identifiable larvae, this means that a larger or smaller number of veligers of the particular species must be assumed to be found in the group of "small indeterminable larvae". If the number is given without further reduction, it has reference to the total number of veligers occurring in the plankton sample of the species in question.

The accompanying drawings in the text have all been drawn by the present author by means of the Abbe drawing apparatus. If the fleshy parts of the larvae are represented, the larvae were always drawn alive. In Fig. 161 the most important organs to be seen in the following drawings of larvae are named.

Taxodonta.

The planktonic larvae known within this order belong to two types, 1) the barrel-shaped larvae, to which belong the hitherto described larvae of *Nuculidae* and *Ledidae*, and 2) the veligers characteristic of the rest of the *Taxadonta* as well as of all the pelagic young stages of the remaining marine Lamellibranchs.

Nuculidae.

The peculiar larval stage of the *Nuculidae* was first described by Drew (1899b and 1901). The pelagic larvae do not swim, as normally, by means of a velum, but are entirely surrounded by a ciliated epithelium (the test), which decays when the larva passes into the post-larval stage. Drew identifies the test with the velum, since, like the latter, it issues from the apical field, whence it spreads like a mantle around the whole animal. On the decay of the test, remnants of it, resembling a velum in reduction, may be observed around the apical field.

Drew describes the development of *N. delphinodonta* and *N. proxima* near the coast of Maine. *N. delphinodonta* has an egg size of 210 μ in diameter, and has no pelagic development. In *N. proxima* the egg diameter is 90 μ, and its development passes through a pelagic stage. The time of development from fertilisation to metamorphosis is sixty hours.

Nucula larvae have never been met with in the plankton of the Sound. According to the information given in the literature as regards the egg sizes and maximum larval sizes it must, indeed, be expected that the Nuculids occurring in the Sound have either a very short or no pelagic stage.

Nucula tenuis (Montagu). Rather common in the northern part of the Sound. Found down to some distance south of Ven.

Reproduction: Literature. Egg diameter 120—140 μ. Development undoubtedly non-pelagic or with a very short pelagic stage (THORSON 1936).

Nucula nitida SOWERBY. Found in the Sound to some distance south of Ven.

Reproduction: Literature. The species spawns in the winter near Plymouth. Egg diameter 90 μ. Development not described, but the larva is pelagic (LEBOUR 1938 a).

Nucula nucleus (L.). Rather rare in the northern part of the Sound.

Reproduction: Literature. Egg diameter in the Kattegat c. 180 μ (THORSON, unpubl.). Spawns near Plymouth from spring till early autumn. Egg diameter 100 μ. Development not described, but the larva is pelagic (LEBOUR 1938 a). The prodissoconch measured on a drawing in BERNARD (1898) was 180 μ long. It may therefore be taken for granted that the pelagic stage of this species is very short.

Ledidae.

Of the Ledids only the larva of *Yoldia limatula* has been described (DREW 1899 a and b). The egg is 150 μ in diameter. The larva resembles the *Nucula* larva very much. It has a short pelagic stage. Ninety to one hundred and twenty hours after fertilisation it descends to the bottom; it is then c. 200 μ long, and the test decays in a few minutes.

Leda pernula (MÜLLER). Common in the northern part of the Sound as far as Ven.

Reproduction: Literature. Egg diameter 120—140 μ. Development non-pelagic or with a very short pelagic stage (THORSON 1936).

Leda minuta (MÜLLER). Rather common in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Since no description of a *Leda* larva is available in the literature, we do not know whether it belongs to the barrel-shaped type, though this might be assumed owing to its close relationship to *Yoldia*. It should, however, be borne in mind that another taxodont Lamellibranch group, the *Arcidae*, has a veliger of a normal appearance, which according to the descriptions by ODHNER (1914 a) and YOSHIDA (1937 a) much resembles Mytilid and Pectinid veligers. Like these, the *Arcidae* have a taxodont larval hinge and an eye spot. Thus, though we cannot say beforehand what a *Leda* larva is like, it is improbable that such a larva should have occurred in our plankton samples from the Sound. We never saw a larva with a test, and among the few so far undetermined larvae registered there is none which one might expect would prove to be the larva of a *Leda* species. Considering the frequency of the species, it seems most probable that the pelagic stage, if any, is very short.

Anisomyaria.

In all the species of *Anisomyaria* with pelagic larval stages hitherto described, these stages have a distinct taxodont hinge, several statoconians in the statocyst, and, with a very few exceptions (*Lima*), an eye spot.

Anomiidae.

The larvae have been described by STAFFORD (1912) (*Anomia aculcata*), ODHNER (1914 a) (*A. ephippium*), MIYAZAKI (1935) (*A. lischkei*), and LEBOUR (1938 a) (*A. squamula*).

Anomia squamula L. Rather common in the northern part of the Sound.

Reproduction: A. Literature. The larva was first described by Lebour. At Plymouth the veliger occurs in the plankton throughout the year. The breeding is most intense in autumn and winter. Dons (1936) states that in southern Norway the attachment of young takes place with a very distinct maximum in a single month, either August or September. The attachment took place only during three months.

B. Own remarks. The larva of *A. squamula* has a very characteristic appearance (fig. 162 A). The umbo of the right shell is not developed. The pedal sinus in the right shell is supposed to be initiated in early larval life and is very distinct at the stage of metamorphosis. The larval hinge is taxodont (fig. 162 B) with 3—5 well developed teeth on either side of an intermediate area with very small regular teeth. The shell is of a deep flaxen to orange colour (some few individuals with colourless shells were, however, observed. They may possibly belong to the next species). Prod. I is 65—75 μ long (five measurements). The largest larvae in the plankton may attain a length of c. 250—270 μ. The size at metamorphosis is stated by Lebour to be c. 180 μ, while Stafford as regards the *A. aculeata* veliger figures a stage, still pelagic, of a length of c. 315 μ. However, metamorphosed individuals with prodissoconchs c. 280 μ long were observed in the same locality (west coast of Canada).

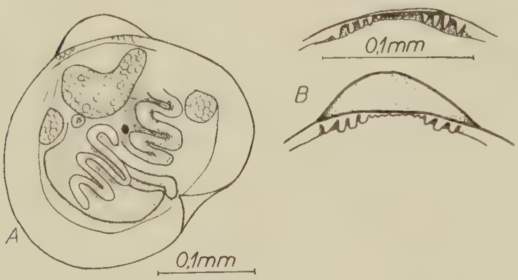

Fig. 162. *Anomia squamula* L. — *A.* Veliger, c. 265 μ in length, from the Sound off Helsingor, $^{2}/_{12}$-1941. — *B.* The hinge of an older veliger. Above the right, and below the left part of the hinge.

The larva occurs in the Sound nearly all the year round. However, hardly any veligers occur from January to June. The main spawning takes place from July to September. A secondary larval maximum in November and December was, however, observed, both in 1938 and 1941 (100 identifiable individuals in a main series taken on Nov. 11, 1941. Cf. also the table on p. 311).

Anomia patelliformis L. Rather rare in the northern part of the Sound.

Reproduction: A. Literature. On the basis of examinations of young bottom stages Bernard (1896) states that this species has a pedal sinus in both valves of the prodissoconch, which was c. 280 μ long.

B. Own remarks. The individuals with colourless shells mentioned under *A. squamula*, which might for that reason be supposed to belong to another species and accordingly, as the only other possibility, to *A. patelliformis*, had only the usual indentation in the right shell. Most probably we are only concerned with a colour variant of *A. squamula*, and thus the veliger of *A. patelliformis* has not been identified in the plankton of the Sound.

Pectinidae.

The reproduction in the *Pectinidae* has been treated by Fullarton (1890) (*Pecten opercularis*), Drew (1906) (*P. tenuicostatus*), Odhner (1914 a) (*P. glaber*), Amirthalingam (1928) (*P. opercularis*), Gutsell (1930) (*P. irradians*), Priol (1930) (*P. maximus*), and Dalmon (1935) (*P. varians*). Apart from the description by Odhner neither descriptions nor drawings of older Pectinid veligers serviceable in identifications of larvae in the plankton are available.

Three undoubted Pectinid larvae have been registered from the Sound. However, we may count upon meeting at any rate four different *Pecten* larvae in the plankton in the northern part of the Sound, since four species of *Pecten* occur here, viz.

Pecten septemradiatus Müller. Rather common in the northern part of the Sound. Extremely common locally in southeastern Kattegat.

Reproduction: A. Literature. Nothing known.

B. Own remarks. The egg size is unknown, but judging from the size of the prodissoconch in quite young individuals from the Kattegat (material kept in the Zoological Museum of Copenhagen) the development must be assumed to be pelagic, for the length of the prodissoconch varied from c. 260 to 325 μ (averaging c. 300 μ — 12 individuals measured). In view of the fact that *P. septemradiatus* is extremely common a little north of the locality in which our plankton samples were taken near Helsingør and is altogether the commonest Pectinid in the northern part of the Sound, it must at the outset be regarded as probable that the Pectinid larva which is most numerous in the plankton belongs to this species. Actually only one Pectinid larva occurred in large numbers in our samples (up to 40 identifiable individuals in a main series) (fig. 163 A), while the other two Pectinid veligers present did not exceed ten identifiable individuals in a main series. This, the most frequent, *Pecten* larva was found in a metamorphosed state in the bottle collectors near Ven in October 1939 in fairly large numbers (c. 20). The young were not so large that their species could be determined, but the shape and size of the prodissoconchs agreed well with the aforementioned young of *P. septemradiatus*. The length of the prodissoconch varied from 250 to 290 μ, with an average length of 275 μ (13 measurements). In addition to these "positive" indications of the species the principle of elimination may be employed. Besides the present larva only two undoubted Pectinid larvae have been found in our samples. Only one of these is of fairly frequent occurrence. It may, however, be referred with fairly great certainty to *P. opercularis*. The other veliger is rare and may moreover be referred with nearly absolute certainty to *P. striatus*. Finally it should be pointed out as improbable that the dominant *Pecten* larva in the plankton should belong to the last *Pecten* species occurring in the Sound, viz. *P. tigrinus*. At the outset it would not be assumed that the veligers of this species, if any, were much more frequent than the *P. striatus* veliger, which was only occasionally found in our samples. For the sake of completeness two further species of *Pecten* may be mentioned whose veligers might be supposed to spread to the Sound even though the adults have not been found alive there. These are *P. similis*, which has been found up to a little south of Anholt, and *P. testæ*, which is of scattered occurrence in eastern Kattegat. Dead shells of this species were taken as far south as Ven. It must be regarded as impossible that the aforementioned veliger should belong to any of these two species, for the prodissoconch length of *P. similis* is very small (125—150 μ — 7 measurements) and rather small in *P. testæ* also (200—250 μ — 7 measurements).

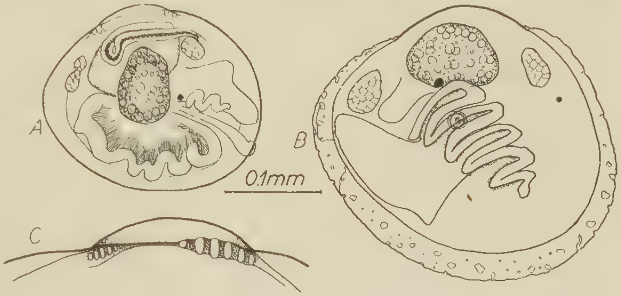

Fig. 163 A-C. *Pecten septemradiatus* Müller. — *A*. Veliger, c. 230 μ in length, from the Sound off Helsingør, $^{17}/_{9}$-1941. — *B*. Young post-larva c. 325 μ in length (prodissoconch c. 290 μ) from the bottle-collectors off Ven, $^{22}/_{10}$-1939. — *C*. Right part of the hinge from the specimen seen in fig. 163 B.

The larval outline of the *P. septemradiatus* veliger is egg-shaped with the pointed end anteriorly (fig. 163 A). The umbos are low and situated rather far forward. The taxodont hinge is divided into a posterior and an anterior part with an intermediate toothless part (fig. 163 C). The left shell is more vaulted than the right one. The ventral parts of the shells are orange-coloured, while the dorsal and central parts are colourless. At intense transmitted daylight the umbos exhibit a deep dark-brown to reddish-brown colour. Five measurements of prod. I showed a length varying from 77—84 μ. Fig. 163 B shows a young bottom stage with a peculiar "hollowed" structure of the incipient dissoconch. A similar structure is found in the post-larva of *P. glaber* figured by ODHNER.

The larva occurs in the plankton from September to November (cf. table 311).

P. opercularis (L.). Rather common in the northern part of the Sound.

Reproduction: A. Literature. The larval development has not been described before, but information is available about the spawning of the species. FULLARTON (1890) states that the egg diameter is 68 μ. Spawning takes place (Firth of Forth) in July-August; sexually mature individuals were, however, found as early as the end of February. In September-October only a few mature individuals were found. Near Plymouth the spawning, which shows correlation with the phases of the moon, takes place from January to June (when the temperature is below 11° C.). Spawning also takes place, though to a less extent, in July and in September-October (AMIRTHALINGAM 1928). According to AMIRTHALINGAM the size of mature eggs is 80—100 μ.

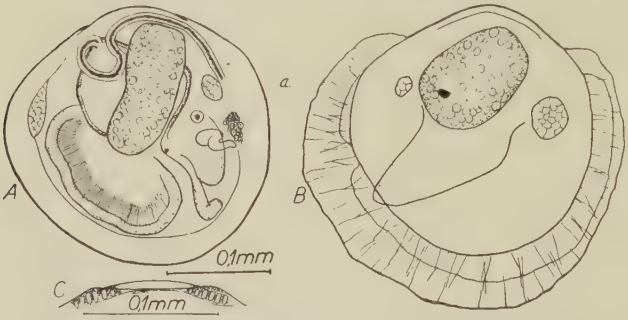

Fig. 164 A-C. *Pecten opercularis* (L.). — *A.* Veliger, c. 260 μ long, from the Sound off Ven, $^{13}/_{9}$-1937. a. brown-coloured structure in the mantle. — *B.* Young post-larva c. 330 μ long, from bottle-collectors off Ven, $^{22}/_{10}$-1939. — *C.* Right part of the hinge of an old veliger.

Own remarks. The nextcommonest *Pecten* larva occurring in the plankton of the Sound is probably the veliger of *P. opercularis*. This is principally suggested by the great similarity that exists between the prodissoconchs of the young identified bottom stages and the plankton larvae. The length of the prodissoconch of the young bottom stages and the largest plankton stages is c. 250—260 μ. The outlines of the shells of the prodissoconchs of the young bottom stages and the plankton veligers are of the same type. As regards the other indications of the correctness of the identification the reader is referred to our remarks under *P. septemradiatus*.

The *P. opercularis* veliger is readily recognisable in the plankton (fig. 164 A). It is about as high as long. The anterior end is pointed, the posterior end very blunt. The umbos are flat and but little projecting. The right shell-half is flat, while the left half is more, though only slightly, vaulted. The taxodont hinge is divided into an anterior and a posterior part with an intermediate toothless area (fig. 164 C). The peripherical portions of the shells are deeply orange-coloured, while the area around the digestive diverticulum is almost colourless. In the individuals hitherto observed a liver-coloured area (in the edge of the mantle?) was always found below the posterior adductor. Fig. 164 B shows a young bottom stage with a characteristic irregular radial striation in the incipient dissoconch.

The *P. opercularis* veliger has been met with in the plankton in the months August-October, but never in large numbers (less than ten identifiable individuals per main series), nor did it occur regularly in each main series within the period in which it may be met with (see further the table on p. 311).

P. tigrinus Müller. Rather rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. The development must be assumed to be pelagic, the length of the prodissoconch in young bottom stages being c. 295 μ (8 measurements, varying between c. 270—310 μ). The prodissoconch had the characteristic pointed anterior end and blunt to flat posterior end found in the other identified *Pecten* larva from the Sound, and the right shell is likewise flatter than the left shell. The veliger has not been observed with certainty in the plankton.

P. striatus Müller. Rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

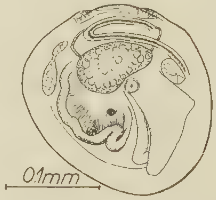

Fig. 165. *Pecten striatus* Müller. — Veliger c. 210 μ long, from the Sound off Helsingør, $^{17}/_{9}$-1941.

B. Own remarks. The veliger of *P. striatus,* which was only taken in a few specimens in the Sound during the years our plankton investigations were carried on, has been identified with great certainty by means of comparisons with the prodissoconchs of quite young individuals found in the collections of the Zoological Museum of Copenhagen. Two of the veligers found were near the stage of metamorphosis (large well developed foot) and measured 210 and 220 μ respectively. The length of the prodissoconch of the young bottom stages varied between 175 and 210 μ (10 measurements), which must be said to be a good agreement. Moreover the shape of the shells of the plankton stages and the prodissoconchs of the young showed close agreement. The only other *Pecten* larvae to which the aforementioned veliger might be supposed to belong are *P. testæ* and *P. similis,* both of which occur in the Kattegat, but have not been taken alive in the Sound (see also under *P. septemradiatus*). Examinations of the prodissoconch of young bottom stages showed that the veliger of *P. testæ* has an oblong shell outline (length 200—250 μ — 7 measurements), the veliger of *P. similis* is likewise oblong, and moreover the prodissoconch is very small (length 125—150 μ). Thus both these possibilities must be excluded.

The shell of the *Pecten striatus* veliger has a very characteristic outline, being shaped like an equilateral triangle (fig. 165). Unlike what was the case in the above-mentioned *Pecten* larvae, the shells are equally vaulted, but very flat. The central area of the shells is colourless, while the peripheric parts are reddish-brown. The veliger has a normal taxodont hinge, very similar to the *P. opercularis* hinge, a strongly developed eye spot, and a statocyst with from one to many statoconians. On the individual drawn here (fig. 165), which was 210 μ long, no gills were observable; this was, however, the case on an individual previously drawn, which was 220 μ long.

The larva was found on a few occasions in the plankton, viz. on Sept. 4, 1937 (one individual), Sept. 17, 1941 (two individuals), and Sept. 5, 1942 (one individual).

Limidae.

The very characteristic veligers have been described by Odhner (1914 a) (*Lima inflata*), Miyazaki (1935) (*L. basilanica*), and Lebour (1937 c) (*L. hians*).

Lima loscombi Sowerby. Not common in the northern part of the Sound, but numerous in certain localities in southeastern Kattegat.

Reproduction: A. Literature. Nothing known.

B. Own remarks. In the autumn the plankton contains fairly large numbers of veligers of a *Lima* species, which can only be *L. loscombi*, for of the other two *Lima* species which have been found in the Danish waters, *L. gwyni* and *L. subauriculata*, only very few specimens were collected in addition to a single shell near the Fladen in the southernmost part of the Kattegat. The specific identity of the *Lima* larva found in the Sound is therefore beyond doubt.

Like the veligers of the other *Lima* species described, the larva of *L. loscombi* is almost of the shape of an equilateral triangle with the umbos at one of the points of the triangle (fig. 166). Six measurements of prod. I gave the lengths 76, 87, 88, 89, 89, and 89 μ. The shells are colourless except for the umbos, which are distinctly reddish. At intense transmitted daylight a red pigment may, in addition, be observed along the hinge. The soft parts of the larva are otherwise colourless and highly transparent. The hinge is normally taxodont, and many statoconians are found in the statocyst, whereas the eye spot is lacking in the *Lima* larva. The exact size at the transition to the bottom stage is not known, but larva in the plankton of a length of well over 300 μ have already developed a strong foot and are hardly far from metamorphosis.

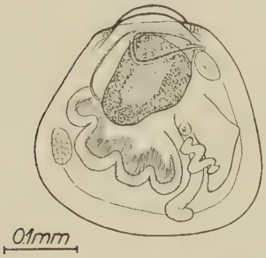

Fig. 166. *Lima loscombi* Sowerby. — Veliger c. 310 μ long, from the Gullmarfjord, Sweden, 22/7-1939.

The larva occurs very regularly in the plankton every year from the end of July, August, or the beginning of September to October-November; occasional individuals may be found as late as December. The larvae may be fairly numerous (more than 300 identifiable individuals have been found in a main series from Ven, Aug. 13, 1938). (See further the table on p. 311.)

Mytilidae.

A large number of papers is available on the reproduction and larval development of the *Mytilidae*. By far the majority, however, deal with *Mytilus edulis*, thus for instance the papers by Delsman (1910), Stafford (1912), Odhner (1914a), Field (1923), and Kändler (1926), while those of Miyazaki (1936a) and Yoshida (1936) deal with *M. crassitesta*, that of Yoshida (1937b) with *Brachidontes senhausi*, and that of Lovén (1848b) with *Modiolaria marmorata*.

Crenella decussata (Montagu). Rather rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. The outline of the prodissoconch is very similar to that of the adult shell. The prodissoconch is c. 750 μ long. A veliger of this size has never been met with in the Sound.

Mytilus edulis L. Common throughout the Sound.

Reproduction: A. Literature. The larva of *M. edulis* is one of the most frequently described Lamellibranch veligers. Of the papers from recent times the following may be mentioned: Borisjak (1909), Stafford (1912), Odhner (1914a), Kändler (1926), and Werner (1939). The egg diameter is 70 μ (Williamson 1907, Field 1923, and Battle 1932)[1].

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[1] John Wilson (1887) reports the egg diameter to be 61 μ (Scotland); he likewise states that the size at metamorphosis is 188 μ, that is to say, a smaller size than recorded by any of the subsequent investigators.

The larva occurs near Heligoland from April to December (Kändler). Matthews (1913) assigns the spawning time at Plymouth to January, February, and March. Lebour (1938 a), however, states for the same locality that the veliger is dominant in the plankton in late spring and early summer. In the Black Sea it may be met with all the year round, with a pronounced maximum in July, August, and September (Borisjak). Along the west coast of Canada the veliger occurs from June to late in the autumn (Stafford).

B. **Own remarks.** One of the most remarkable peculiarities of the *M. edulis* veliger, according to our experience, is its excessive variability both as regards the colour of the shell, its shape, and stage of development as compared with the larval size, in which respects it is not surpassed by any of our other common Lamellibranch veligers. Whether this variability is found to the same extent throughout the area of distribution of the species, does not appear clearly from the available literature.

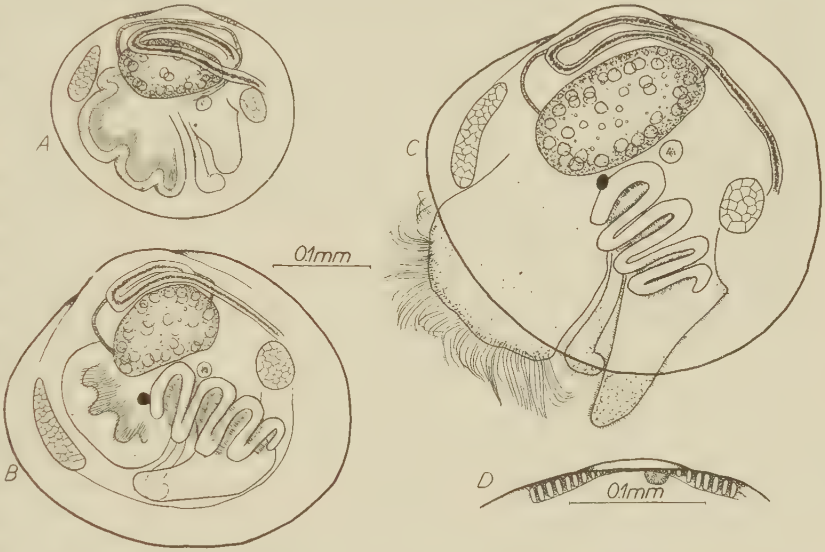

Fig. 167 A-D. *Mytilus edulis* L. — *A.* Veliger c. 245 μ long, from the Sound off Ven, $^{5}/_{8}$-1939. — *B.* Veliger c. 360 μ long, from the Sound off Helsingor, $^{19}/_{12}$-1941. — *C.* Veliger c. 400 μ in length, from the Sound off Ven, $^{6}/_{8}$-1937. — *D.* The right part of the hinge of an old veliger.

In our waters the shape of the larval shell is mostly the egg-shape usually indicated with the pointed end in front (fig. 167 A), but in individuals approaching the stage of metamorphosis the blunt end may often be observed to be, as it were, drawn towards the ventral side, the outline being accordingly more oblique and more like that of the adults (fig. 167 B). As the size on metamorphosis may vary so considerably, it is impossible to indicate precisely the shell shape of the larva at a given size, and even individuals 400 μ long may still exhibit the egg-shape (fig. 167 C).

The great variation in size on metamorphosis is accompanied by great differences in the stage of organisation attained at a certain larval size. Thus, for instance, larvae c. 250 μ long, near the size of metamorphosis, will be relatively dark and opaque, with well developed gills and foot and with a velum in reduction, while larvae of the same size, far from the size of metamorphosis, will be much paler and more transparent, with smaller incipient gills and foot, and with a large velum. All the transitional stages between the extreme limits will often be represented in a large collection of larvae from the same plankton sample. The variable size on metamorphosis is accordingly not solely due to the fact that the veliger may pass into the bottom stage after attaining a different stage of organisation, but it is also due to the varying ratio between the rate of differentiation of the tissues and the rate of growth from one individual to the other.

The colour of the veligers may likewise vary considerably. Most frequently the shells of the rather old larvae are of a deep orange colour, and the animal is rather opaque, while the shells of the younger stages are of a lighter colour. But the colour may be pale or entirely absent even in individuals ready to metamorphose. Often the ventral portions of the shell are more intensely coloured, while the dorsal parts are paler. Finally, a large percentage of the veligers may be found to have a more or less strongly purple-coloured anterior end, constituting about one-third of the animal, while the remainder of the shell is orange-coloured. Previously individuals of this type were assumed to belong to *Modiola modiolus*, which is the only other Mytilid which may with some probability come into question, judging from the frequency of the type. However, later measurements of prod. I showed that it was of precisely the same size in the purple-coloured type as in the undoubted *M. edulis* veliger. On account of the larger egg size of *Modiola modiolus* (diameter 100 μ) it is to be expected that the prod. I of its veligers would be somewhat larger than that of the *M. edulis* veligers. There can be no doubt, therefore, that the veligers with the purple-coloured anterior ends also belong to *M. edulis*. Gradual transitions between purple-orange and purely orange-coloured shells were likewise observed. However, a blue colour of the posterior parts of the veliger shells, as recorded by BORISJAK and WERNER (l. c.), was never observed.

The average length of prod. I is 103 μ (varying from 90—112 μ in 62 measurements). WERNER records the average length as 113 μ (average of 100 measurements), but he says nothing about the range of variation (see also p. 279). The larval hinge has previously been described by BORISJAK and WERNER. It is taxodont, with 6–8 strong teeth on either side of an intermediate area with very small teeth situated just below the umbos. The ligament is situated some distance behind the middle of the hinge (fig. 167 D).

The veligers begin to appear in the Sound at the end of May or the beginning of June. As a rule they suddenly appear in large numbers, and dominate in the plankton throughout the summer. (About 10,000 individuals were found in a single main series in the month of July 1939.) In September-October the veliger decreases considerably in number, though it may be fairly frequently met with until December-January, and even in the months of spring occasional individuals may be observed (see also the table on p. 311). In the Isefjord, also, the *Mytilus* veliger appears at the end of May. Here the spawning is very rapidly completed, for as early as the end of June almost only individuals of the metamorphosis size are met with, and about the middle of July no more larvae occur in the plankton.

Modiola adriatica LAMARCK. Rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. The examination of a couple of young bottom stages would seem to suggest that the development is non-pelagic, for the prodissoconch in these specimens was found to be c. 1 mm long. However, growth lines, delimiting an area c. 400 μ in length, were observed on the prodissoconch. There might thus be a possibility that a pelagic stage, if any, would be completed at this length, but that the prodissoconch then continues its growth, to be replaced, at a length of c. 1 mm, by the adult shell type. Parallel cases to such a shell formation are, however, not known, and since, moreover, the growth line in one of the individuals was double, it is not very probable that it should mark the end of a pelagic stage. Most probably the large prodissoconch had been formed by a non-pelagic larva on the basis of a large egg rich in yolk.

Modiola phaseolina PHILIPPI. Rather rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Nothing known.

Modiola modiolus (L.). Common locally in the northern part of the Sound.

Reproduction: A. Literature. The development is not known. Near Scotland the spawning takes place at any rate from April to June (at the same time as *Mytilus edulis*). The egg size is stated to be 100 μ (Williamson 1907).

B. Own remarks. Sexually mature individuals have been found in the Little Belt in the month of July. Egg diameter c. 100 μ. Measurements of the prodissoconchs of young bottom stages all showed a length of c. 400 μ (4 measurements). The larva has not been identified with certainty in the plankton of the Sound. Possibly the resemblance to the *M. edulis* veliger may be so great that a confusion of these two species may have taken place (cf. *M. edulis*). Artificial fertilisation successful (Kristineberg, July 1946, inform. from Prof. J. Runnström).

Modiolaria marmorata (Forbes). Rather rare in the northern part of the Sound.

Reproduction: A. Literature. Lovén (1848b) observed spawning in the summer, first by males and subsequently by females, in aquarium experiments (Kristineberg). The egg diameter is stated to be 0.02 mm; however, this must be due to a misprint. The larval development was followed to the youngest shell-bearing stages, 0.08 mm long.

B. Own remarks. Sexually mature individuals were found in the northern part of the Little Belt at a depth of c. 50 m on July 26, 1944. They were observed spawning in the laboratory. Egg diameter c. 58 μ. Some few bottom stages of *M. marmorata* were found in the bottle collectors in October 1939. The very characteristic prodissoconch made it possible to trace back the species with certainty to the planktonic stages.

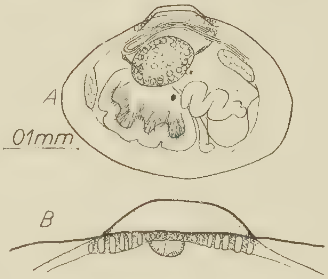

Fig. 168. *Modiolaria marmorata* (Forbes). — *A*. Veliger c. 300 μ long, from Gullmarfjord, Sweden, $^{26}/_{7}$-1939. — *B*. The left part of the hinge of a young post-larva c. 400 μ long with a prodissoconch measuring c. 320 μ in length.

The veliger is triangular and may to some extent resemble a *Nucula* in shape (fig. 168A). However, the umbos, which are flat, are situated nearest the anterior end. The shells are strongly orange-coloured. The umbos and the hinge region are distinctly purple or reddish. In plankton larvae approaching the stage of metamorphosis the taxodont hinge contains 5—7 big teeth in front, above the larval ligament half a score of small rudimentary teeth, and most posteriorly 5—6 big teeth (fig. 168B). Finally, the larva has an eye spot and a statocyst with many statoconians.

The shell area following immediately behind the prodissoconch in the young bottom stage, the so-called interdissoconch, differs conspicuously from the final dissoconch by being colourless and without any radial structure. Not till the larva has reached a length of about 1 mm, will the shell characteristic of *M. marmorata* begin to form.

The largest planktonic stages measured had a length of c. 370—380 μ. The largest prodissoconch measured in metamorphosed individuals was 400 μ long. The veliger may, however, leave the plankton after attaining a somewhat smaller length, young bottom stages whose prodissoconch was only 320 μ long having been met with. The average length ranged between 340 and 370 μ both in the Sound and at the zoological station of Kristineberg, where the veliger was of frequent occurrence in August-September 1939. (It was not under observation outside this period.)

The larva is only of sparse occurrence in the Sound. A couple of individuals were met with in December 1937, and some few in October 1939. Finally, the larva occurred regularly in the plankton off Helsingør in September-October 1941 (up to c. 40 identifiable individuals in a main series (September 1941). (See also the table on p. 311.)

Modiolaria discors (L.). Occurs in the northern part of the Sound.

Reproduction: Literature. The development is non-pelagic. The egg size is 0.30 × 0.22 mm. Egg string found in Holbæk Fjord in May (THORSON 1935b).

Modiolaria nigra GRAY. Common in the northern part of the Sound.

Reproduction: Literature. The development is non-pelagic. The egg size is 0.52 × 0.36 mm (THORSON 1935b).

Eulamellibranchia.

Astartidae.

Astarte borealis (CHEMNITZ). Fairly common, especially in the southern part of the Sound.

Reproduction: Literature. Egg diameter 150—200 μ, larval development non-pelagic (THORSON 1936).

Astarte montagui (DILLWYN). Common throughout the Sound.

Reproduction: Literature. Egg diameter 150—200 μ, larval development non-pelagic (THORSON 1936).

Astarte elliptica (BROWN). Fairly common throughout the Sound.

Reproduction: Literature. Egg diameter 150—200 μ, larval development non-pelagic (THORSON 1936).

Thyasiridae.

Thyasira flexuosa (MONTAGU). Occurs in the northern part of the Sound as far south as Ven.

Reproduction: Literature. Egg diameter 150—200 μ, larval development non-pelagic (THORSON 1936).

Lucinidae.

Lucina borealis L. Rather rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Nothing known.

Montacutidae.

The reproduction and larval development have been treated by LOVÉN (1848b), and LEBOUR (1938a) (*Montacuta bidentata*), and MIYAZAKA (1936b) (*Mysella japonica*).

Montacuta bidentata MTG. Common in the northern part of the Sound, occurring southward to Taarbæk.

Reproduction: A. Literature. The earliest development takes place in the mantle cavity of the mother, whence the veliger is ejected when it is c. 0.15 mm long. Spawning in the summer at Kristineberg (LOVÉN). The planktonic stages have been described by LEBOUR

(1938a). They are reported to have been reared to identifiable stages, and are found in the plankton in the autumn, winter, and spring.

B. Own remarks. It would seem that the correctness of Lebour's determination of the *M. bidentata* veliger might be doubted. For in our opinion it is Lebour's *Mysella* sp. larva (Lebour 1938a, fig. 7d—g) which is identical with the *M. bidentata* veliger. A larva much resembling Lebour's sketch of the *Mysella* sp. larva was found in large numbers in a metamorphosed state in the bottle collectors in the autumn of 1939. The largest post-larvae were 1.2 mm long, and could be identified as *Montacuta bidentata* (fig. 169 A—B).

As long as the *M. bidentata* veliger is less than c. 400 μ in length, it is rather square in outline. The larvae (fig. 169) are colourless and highly transparent. However, in intense transmitted daylight the dorsal edge has a purple tinge. The shells are distinctly concentrically grooved. The hinge has no larval teeth. The lateral teeth are only developed in older planktonic stages near metamorphosis. When ready to metamorphose, the veligers have more opaque and yellowish shells and at the same time the shells become more egg-shaped with the blunt end anteriorly. The umbos are now situated behind the middle of the animal. Prod. I is c. 134 μ long (average of 31 measurements, which varied from 120 to 150 μ).

The metamorphosis may take place at rather different lengths; the largest planktonic stages were c. 550 μ long. Measurements of the prodissoconch of young bottom stages from the Sound, the Little Belt, and Gullmar Fjord show lengths varying between 520 and 440 μ (7 measurements). The size on metamorphosis, however, may no doubt exhibit a still greater range of variation. Lebour records it as c. 320 μ for her *Mysella* sp. larva (while the length on metamorphosis of the larva which she calls the *M. bidentata* veliger is stated to be 340 μ), a length which is considerably below that observed in our waters.

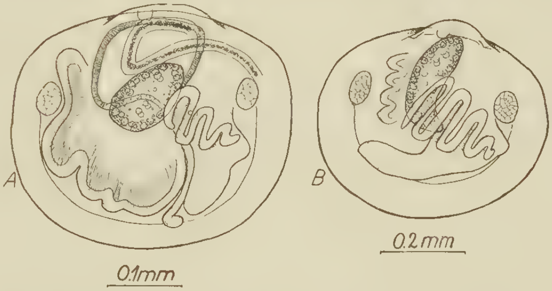

Fig. 169 A-B. *Montacuta bidentata* Mtg. — *A*. Veliger c. 380 μ and *B*. c. 520 μ long, both from Gullmarfjord, Sweden, $^{22}/_{7}$-1939.

At certain times of the year the *M. bidentata* veliger plays an important part in the plankton. It is present from June-July to September-November, though occasional larvae have been met with outside that period, e. g. in January 1942. When the larvae are most numerous in the plankton, up to c. 850 identifiable individuals have been counted in a main series (September 1941). (See also the table on p. 311).

Montacuta ferruginosa (Montagu). Not rare in the northern part of the Sound.

Reproduction: A. Literature. The species is viviparous. Spawning of the veligers, c. 0.14 mm long, was observed at Kristineberg in the summer (Lovén 1848b). The larger veligers have not been described.

B. Own remarks. In the plankton of the Sound a larva was met with which much resembles Lebour's *M. bidentata* larva. This veliger, which is an indubitable *Montacuta* larva, must belong to *M. ferruginosa*, which in addition to the preceding species is the only Montacutid occurring in the Sound. It must be regarded as impossible that it may be the larva of *M. substriata*, which is of very scattered occurrence in eastern Kattegat as far southward as Kullen, and even here it is much rarer than *M. ferruginosa*, considering the large number of larvae which occurred in the autumn of 1941.

The *M. ferruginosa* veliger is colourless and very transparent, and large in relation to the stage of organisation, just as the *M. bidentata* veliger. The young larvae (up to a length of c. 300 μ) are almost egg-shaped, with the blunt end forward (fig. 170 A). Older veligers grow more pointed anteriorly and posteriorly while the ventral edge loses part of its rounding (fig. 170 B–C). The hinge has no larval teeth, but shows incipient lateral teeth in the older planktonic stages. The ligament is well developed.

The larva does not attain the same length in the plankton as the *M. bidentata* veliger, being only about 400 μ long. A single bottom stage measured had a prodissoconch of a length of 400 μ.

The larva was only observed on a few occasions in the plankton off Ven, while in September-October 1941 and from July 1942 it was fairly abundant off Helsingør, up to 150 identifiable individuals having been counted in a main series. (See also the table on p. 311).

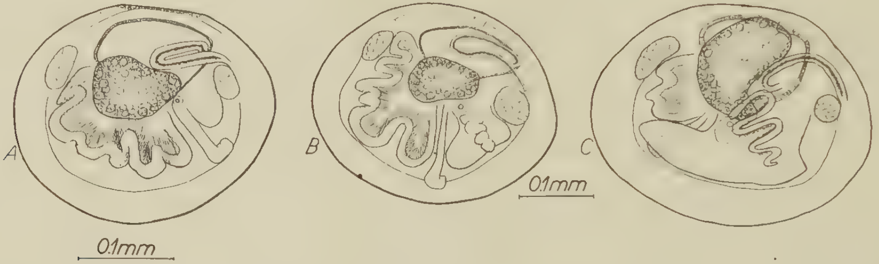

Fig. 170 A-C. *Montacuta ferruginosa* (Mtg.). — *A.* Veliger c. 275 μ long, from the Sound off Helsingør, $^{17}/_{9}$-1941. — *B.* Veliger c. 350 μ long, from Gullmarfjord, Sweden, $^{16}/_{9}$-1939. — *C.* Veliger c. 375 μ long, from Gullmarfjord, Sweden, $^{22}/_{7}$-1939.

Cardidae.

The reproduction and larval development have been treated by Lovén (1848 b) (*Cardium exiguum*), Odhner (1914 a) (*C.* sp.), and Lebour (1938 a) (*C. edule, C. nodosum,* and *Lævicardium norvegicum*).

Cardium echinatum L. Not rare in the northern part of the Sound, occurring as far southward as Rungsted.

Reproduction: A. Literature. Lebour reared a larva from the plankton near Plymouth which is almost indubitably the larva of *C. echinatum.* However, she gives neither a description nor a drawing of the veliger, only a young bottom stage having been drawn. The size on metamorphosis is stated to be c. 480 μ. The veliger occurs in the plankton in spring, summer, and autumn.

B. Own remarks. The veliger was not identified with certainty in the plankton of the Sound.

Cardium minimum (Philippi). Not rare in the northern part of the Sound. Found as far southward as Ven.

Reproduction: A. Literature. Nothing known.

B. Own remarks. The prodissoconch of young bottom stages found in the collections of the Copenhagen Museum measured between 330 and 400 μ, averaging c. 365 μ (12 measurements). The development must therefore be regarded as pelagic. However, the veliger was not encountered with certainty in the plankton of the Sound.

Cardium exiguum Gmelin. Occurs throughout the Sound in very shallow water.

Reproduction: A. Literature. Lovén observed the spawning of the species in the summer months near the coast of Bohuslän. Egg diameter 64 μ. The eggs are laid enclosed in a thick gelatinous mantle, within which the development goes on until the shell-bearing veliger has attained a length of 90 μ. Lovén was unable to follow the development further.

B. Own remarks. It is difficult to delimit the prodissoconch in the young bottom stages, there being a gradual transition to the final shell type. The length, however, seems to be about 250 μ, but nothing is known about the possible variability in length on metamorphosis. The veliger was not observed with certainty in the Sound.

Cardium fasciatum Montagu. Common in the northern part of the Sound. Found as far southward as Saltholm.

Reproduction: A. Literature. Orton (1924) made successful artificial fertilisation in the month of June of individuals which had passed into the bottom stage on October 22nd, at the earliest, of the previous year. However, the larval development was not observed.

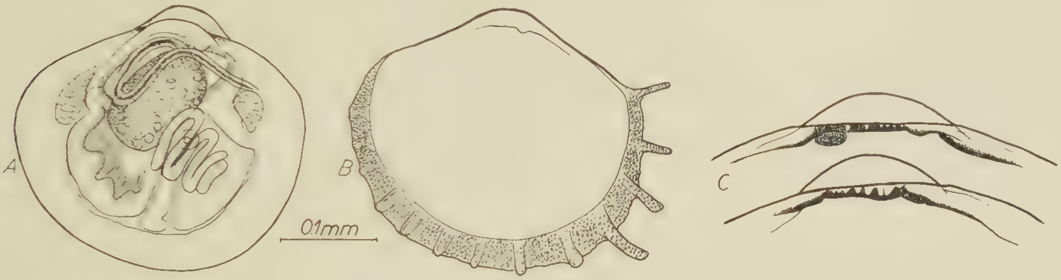

Fig. 171 A-C. *Cardium fasciatum* Mtg. — *A.* Veliger c. 300 μ long, from the Sound off Ven, $^{24}/_{10}$-1939. — *B.* Young post-larva c. 315 μ long, from bottle-collectors off Ven, $^{22}/_{10}$-1939. — *C.* Hinge of old veliger (c. 300 μ long).

B. Own remarks. From young bottom stages (fig. 171 B) taken in the bottle collectors it was possible to trace the species back to the planktonic stages.

The egg is c. 80 μ in diameter. Three measurements of prod. I gave the lengths 93, 95, and 98 μ.

The late veliger (fig. 171 A) has strongly vaulted shells. The umbos are well developed and are situated far apart, a little behind the middle of the animal. The dorsal lines of the shells are straight, and pass rather abruptly into the ventral line, which is almost semicircular (fig. 171 A). The hinge of the late larva shows an incipient final differentiation (fig. 171 C). However, at first the hinge passes through an incomplete taxodont stage. The larval ligament is well developed. The shells are colourless or lightly yellowish. The hinge area may, however, be of a deep reddish or reddish-purple colour. The soft parts even of the oldest veligers are colourless and transparent, though the mantle edge may be rather deeply flesh-coloured.

The largest stages of the *C. fasciatum* larva met with in the plankton of the Sound were c. 300 μ long. Measurements of the prodissoconch of young taken in the bottle collectors show, however, that the veliger may leave the plankton already at a length of c. 255 μ. The length varied between 255 and 320 μ, average c. 300 μ (10 measurements). Unfortunately the larva was not registered regularly near Ven, but it seems to spawn in the late summer and autumn. It was found in a metamorphosed state in large numbers in the bottle collectors in September 1939. Off Helsingør it was found as late as November 1941 and in July-August 1942, and it was fairly abundant in September (c. 300 identifiable individuals in a main series). (See also the table on p. 311.)

Cardium edule L. Common throughout the Sound.

Reproduction: A. Literature. At Plymouth the main spawning takes place in the late spring and during the summer months. Egg diameter 50 μ. Oldest planktonic stages c. 300 μ long (Lebour 1938a). Unfortunately Lebour gives no drawing or description of the veliger that may be used for an identification of the larva, her drawings showing only a rather indistinct shell outline.

B. Own remarks. Veligers were reared by us in aquaria to identifiable stages.

Thirty-one measurements of prod. I gave an average length of c. 105 μ (ranging from 97 to 112 μ).

The shell of the fairly old veliger is elliptic in outline with rather blunt anterior and posterior ends (fig. 172A). The umbos are flat. The shells are flat and fairly distinctly concentrically grooved. The larva is much more opaque than most other Lamellibranch larvae of the same size. It looks very grey at slight magnification, compared with the great majority of other veligers occurring in the plankton of the Sound. The most characteristic feature of the old veligers seems to be a blackish-blue pigmentation of the ventricular wall (fig. 172B). This pigmentation was observed in late larvae both from the Danish waters and from the Gullmar Fjord, but it is not mentioned by Lebour. Such a pigmentation was not observed in other Lamellibranch larvae found in our waters. Even in plankton larvae nearly 300 μ long no differentiation of the hinge was observed.

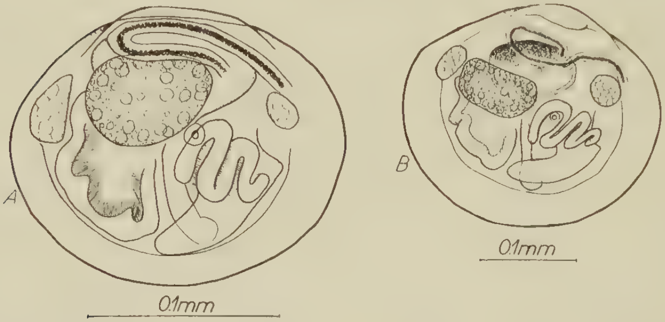

Fig. 172 A-B. *Cardium edule* L. — *A*. Veliger c. 175 μ long, from the South Harbour of Copenhagen, $^{12}/_{6}$-1940. — *B*. Veliger c. 270 μ long, from the Sound off Ven, $^{15}/_{7}$-1939.

The *Cardium edule* larva is distinguished by an excessive variation in the size on metamorphosis. In rearing experiments at Kristineberg the length was found to vary from c. 275 to 345 μ. Length measurements of prodissoconchs of young from the oyster basins in the Limfjord varied from 200 to 275 μ (average c. 240 μ — 13 measurements). The prodissoconch of a young bottom stage derived from the bottle collectors near Ven was 255 μ long, but veligers 335 μ long were encountered in the plankton in the same place. In *C. edule* young from the harbour of Copenhagen (south harbour) a prodissoconch length of c. 225 μ was measured, while in young from the Christianshavn moat (Copenhagen) the length was 150—240 μ.

C. edule spawns in the spring and summer, but a few veligers may be met with as late as October. In July up to 300—400 identifiable individuals were taken in a main series off Helsingør. (See also the table on p. 311.)

Cyprinidae.

Cyprina islandica (L.). Fairly common as far southward as Ven.

Reproduction: A. Literature. Not known.

B. Own remarks. The species was found spawning at Kristineberg in the month of

July. Egg diameter 75 μ. The prodissoconch, measured in quite young individuals, varied between 270 and 300 μ (6 measurements).

Since *Cyprina islandica* is rather common right down to Ven (LOVÉN 1929), we might expect that the veliger would be found in the plankton of the Sound. Possibly the veligers shown in figs. 173 A and B belong to *C. islandica*. Of the three or four veliger types which are of fairly common occurrence in the Sound but not yet identified, this larva is probably the only one which may be the *Cyprina* larva. The veliger is thick and roundish in outline, and the shells are colourless. This is in good agreement with the features which we might expect to find in the *Cyprina* veliger, judging from investigations of the prodissoconch in young bottom stages. The size on metamorphosis would seem to vary rather considerably. In the Sound individuals, up to 325 μ long, of the supposed *Cyprina* larva have been found, while the largest plankton stages in the Little Belt were c. 260 μ long; here the veliger was of common occurrence in July 1944. As will be seen, there is good agreement between the prodissoconch lengths measured in the young bottom stages.

The veliger is characteristic and easily recognisable in the plankton. It is colourless and transparent. In the largest individuals, however, the mantle edge is often flesh-coloured. The digestive diverticulum is mostly of a deep brown colour. The dorsal lines are straight or slightly concave in the largest stages. Weak taxodont teeth are found in the straight larval hinge. In the right valve there occur in addition two distinct, fairly sharp ridges, which run parallel to and a little inside the dorsal shell margins, while the ventral valve is equipped with very thick dorsal margins. These formations occur at any rate in veligers only well over 200 μ long. (Cf. also the *Venus gallina* veliger dealt with below.) Prod. I is c. 86 μ long (average of 24 measurements, which varied from 80 to 95 μ).

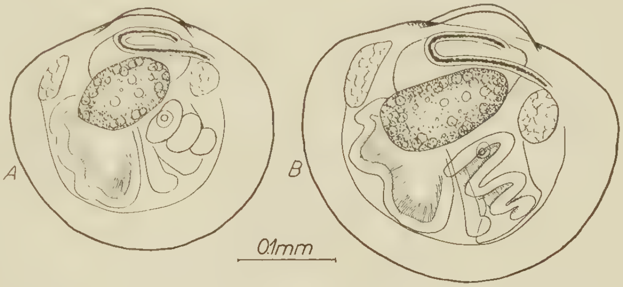

Fig. 173 A-B. Larva probably belonging to *Cyprina islandica* (L). — *A*. Veliger c. 270 μ long, and *B*. Veliger c. 325 μ long, both from the Sound off Helsingør, $^{18}/_{7}$-1942.

The veliger is met with in the plankton in summer and autumn. Up to c. 150 identifiable individuals were found in a main series (September 1942).

Veneridae.

The larval development has been described by STAFFORD (1912) (*Venus mercenaria*) and YOSHIDA (1935) (*Venerupis philippinorum*).

Lucinopsis undata (PENNANT). Rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Egg diameter 65—70 μ (Kristineberg). The species must therefore be assumed to have a pelagic development. The veliger was not identified in the plankton of the Sound.

Venus gallina L. Occurs as far southward as Helsingør and Ven.

Reproduction: A. Literature. Larval development not described. LEBOUR (1938 a) states that the species spawns at Plymouth in February, March, and May. Artificial fertilisation was successfully accomplished in February and May, but the larva was only followed to early swimming, but not identifiable stages.

B. Own remarks. A few bottom stages, fairly certainly the young of *V. gallina*, were found in the bottle collectors off Ven in the summer of 1939. The dissoconch had deep concentric grooves, and the hinge was provided with strong, but not yet characteristic teeth. In definitely identified young of *V. gallina* the characteristic deep grooves were seen to arise immediately behind the prodissoconch. The veligers which belong to the young found in the bottle collectors, are not very characteristic but of varying appearance. Moreover they leave the plankton rather early. Hence they have no doubt often been overlooked among the Lamellibranch larvae in previous years.

The diameter of the egg of *V. gallina* is 70—80 μ. A single prod. I measured was 108 μ long. The larval outline varies from almost square to circular. The shell is mostly of a deep flaxen colour, especially the ventral parts, but the larva may also be almost colourless. All transitions may be found. The shells are distinctly concentrically grooved. The umbos are low, with a distinctly punctate structure. At intense transmitted daylight the whole animal is of a faint reddish colour (fig. 174). In the right valve some distinct ridges are found within the dorsal shell margins on either side of the umbo. To these ridges correspond some protuberances of the dorsal shell margins of the left valve. The ridge and the marginal thickenings are especially marked behind the umbos. Below the umbos a number of rudimentary teeth are found.

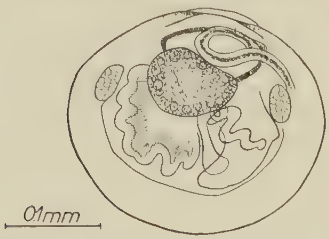

Fig. 174. *Venus gallina* L. (?) — Veliger c. 270 μ long, from the Sound off Ven, $^{24}/_{10}$-1939.

Larvae c. 270 μ long were met with in the plankton. The prodissoconch of a young bottom stage derived from the bottle collectors was 280 μ long. The larva may, however, metamorphose at a much smaller size. In three young from the Kattegat the length of the prodissoconch varied from 210 to 225 μ.

The larva of *V. gallina* occurs in the plankton of the Sound in the summer and autumn months; it is often fairly common, thus in October-November 1941 up to 800 identifiable individuals were found in a main series off Helsingor. In 1941—42 it was found as late as February. (See also the table on p. 311.)

Venus ovata Pennant. Fairly common in the northern part of the Sound.

Reproduction: A. Literature. Egg diameter in the Kattegat c. 50 μ (Thorson, unpubl.). The veliger is not known. Spawning at Plymouth from March to October (Lebour 1938).

B. Own remarks. Six prodissoconch measurements in young bottom stages gave the values 200, 210, 210, 210, 220, and 250 μ. Veligers not identified in the plankton of the Sound. Have perhaps been confused with *V. gallina*.

Tellinidae.

Reproduction and larval development treated by Odhner (1914 a) (*Tellina* sp.), Battle (1932) (*Macoma baltica*), Miyazaki (1938 a) (*T. juvenalis*), and Werner (1939) (*M. baltica*).

Macoma baltica (L.). Common in shallow water throughout the Sound.

Reproduction: A. Literature. Egg size 80 × 60 μ (Battle 1932). The veliger has been described by Werner from the southern part of the North Sea. He records the length of prod. I as 150 μ, while the veliger ready to metamorphose is 294 μ.

B. Own remarks. See below (pp. 297—300).

Macoma calcarea (Chemnitz). Common throughout the Sound.

Reproduction: A. Literature. Egg diameter 170 μ. Development non-pelagic (Thorson 1936).

Tellina pusilla Philippi. Rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Nothing known.

Tellina tenuis Da Costa. Occurs in southern Kattegat, rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Nothing known.

Tellina fabula Gronovius. Fairly common in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. See below (pp. 297—300).

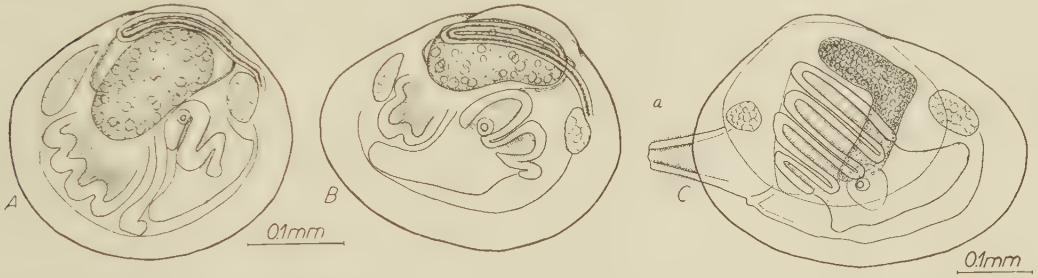

Fig. 175 A-C. *Macoma baltica* (L). — *A*. Veliger c. 295 μ long, from the Sound off Ven, $^{30}/_{4}$-1939. — *B*. Veliger c. 315 μ long, from the Sound off Ven, $^{15}/_{7}$-1939. — *C*. Young post-larva c. 460 μ long (prodissoconch c. 310 μ) from Gullmarfjord, Sweden, taken at a depth of c. 20 cm, a. exhalating siphon.

Semelidae.

Larval development described by Kändler (1926) (*Syndosmya alba*) and Grave (1927) (*Cumingia tellinoides*).

Syndosmya nitida (Müller). Fairly common in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. See below (pp. 297—300).

Syndosmya alba (Wood). Common throughout the Sound.

Reproduction: A. Literature. The veliger has been described by Kändler from Heligoland, but it is impossible to identify with certainty the larva from the plankton of the Sound on the basis of his drawing and description. Kändler found the larva to be numerously represented in the plankton, especially in November, but also in December. The size on metamorphosis was c. 300—320 μ.

B. Own remarks. See below (pp. 297—300).

Since 1937 a larval type has been registered in the lists under the designation "dirty Lamellibranch larva". To this were referred obliquely oval to nearly triangular larvae which differed from the other Lamellibranch veligers occurring in the plankton samples in that dirt was always attached to the surface of their shells. This group of "dirty larvae" has later proved not to be homogeneous, including veligers of *Macoma baltica*, *Tellina* sp. (probably *T. fabula*, since this is by far the commonest Tellinid in the Sound), and no doubt also *Syndosmya* sp. There is no possibility that other species of Lamellibranchs than those just mentioned should be represented[1]).

The greater number of the "dirty larvae" which occur in the plankton in the months of spring and the early summer must be assumed to belong to *M. baltica*. The drawings of larvae available from the month of April (fig. 175 A) show good agreement with Werner's drawings of the *M. baltica* veliger. However, the oldest veligers taken in the Sound have more triangular shells than recorded by Werner for the veligers ready to descend to the bottom (fig. 175 B). They may assume the triangular outline when they have attained a length of c. 290 μ. Thus already in the plankton the larvae may be very similar in shape to the young bottom stages. A post-larva c. 460 μ long is shown in fig. 175 C. In the triangular stage the veligers of *M. baltica* are easily distinguishable from the more oval veligers of *Tellina* and *Syndosmya*. The larva of *M. baltica* attains a length of c. 310 μ in the plankton, a size which agrees entirely with the largest prodissoconchs measured in young bottom stages. However, we know very little about the range of the variation in size on metamorphosis in our waters.

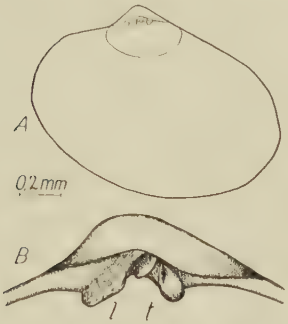

Fig. 176 A-B. *Syndosmya* sp. *A*. The left valve of a post-larva c. 1,2 mm long, and *B*. The left part of the hinge from a specimen c. 1 mm long, both from bottle-collectors off Ven in July 1941. l. ligament, t. teeth.

As mentioned above, Werner states that prod. I is 150 μ long. However, the largest prod. I measured in *M. baltica* veligers from the Sound was only 148 μ, and lengths down to c. 115 μ have been observed. Thus, as regards this species, also, the length of prod. I exhibits much greater variations than would appear from Werner's investigations.

Incipient elements of the final hinge are found in the older veligers in the shape of a big conical pointed tooth situated most anteriorly in the left valve or in both valves, as already described by Werner. But both *Tellina* and *Syndosmya* start with hinge differentiations of precisely the same appearance. Accordingly this character cannot be used for a distinction of the species in the veliger stage.

The old *M. baltica* veligers are rather opaque and have dirty-yellow shells; as mentioned above, the shells in the plankton samples are always found to be covered with dirt. The area around the umbos appear distinctly reddish at intense transmitted daylight. The colour of the digestive diverticulum is very often yellowish-green to clear green, but may also be yellowish-brown.

The veliger of *M. baltica* occurs in the plankton from April-May and has been found as late as the middle of August (drawings of the larva are available from August 13th). It is difficult to decide, however, how large a proportion of the group "dirty larvae" taken in June-July should be referred to the *M. baltica* veliger and how large proportions to *Tellina* and *Syndosmya*, nor is it possible to determine the ratio between the two latter groups among the "dirty larvae" occurring in autumn and winter. It seems most likely, however, that *Syndosmya*, in particular, occurs in the months of June and July in addition to

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[1]) At first we suspected the group to be identical with *M. baltica*, since in the summer the "dirty larvae" occurred in purely Baltic water in company with the veligers of *Cardium edule*, *Mya arenaria*, and *Mytilus edulis*.

M. baltica, while *Tellina* does not appear in company with *Syndosmya* till the month of August, at the same time as *Macoma* disappears. This seems to be evident from the below:

Bottle collectors exposed at a depth of c. 16 m off Ven from May 27th to July 20th, 1941, were found to contain c. 75 metamorphosed individuals of the "dirty" larval type. A single individual was c. 1.2 mm long, while by far the greater number ranged from such as had just descended to the bottom to such as were up to c. 0.7 mm long. On the basis of the well developed internal ligament the largest individuals could be identified with certainty as *Syndosmya* (see figs. 176 A and B). The prodissoconch varied between 310 and 375 μ (average 335 μ — 11 measurements), while prod. I ranged between c. 100 and c. 115 μ (6 measurements). Whether we are here concerned with *S. alba* or *S. nitida*, or both, it is impossible to decide on the basis of the available material. The two forms have prodissoconchs of about the same length, thus seven measurements of young bottom stages of *S. nitida* varied between 285 and 350 μ, a single prodissoconch measured in *S. alba* was c. 350 μ long. (As mentioned above, Kändler states that near Heligoland *S. alba* metamorphoses when it is c. 300 μ long). If we are to decide the question on the basis of the frequency of the two species in the Sound, it is, no doubt, most likely that the post-larvae of *S. alba* are dominant among the *Syndosmya* individuals found at the bottom of the bottle collectors.

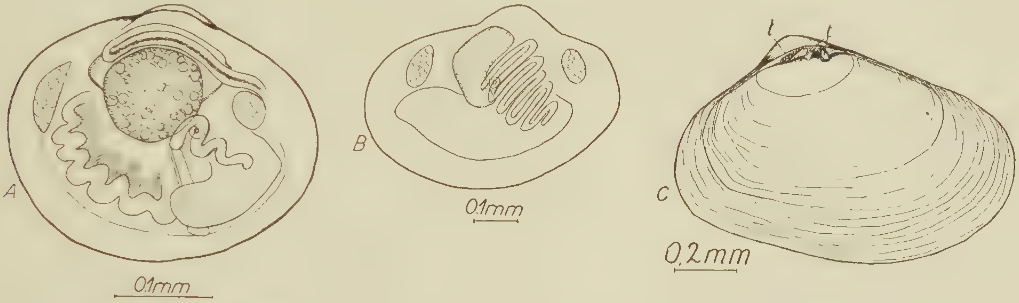


Fig. 177 A-C. *Tellina* sp. — *A.* Veliger c. 320 μ long, and *B.* Post-larva c. 550 μ long, both taken in the same plankton sample from the Sound off Helsingør, $^{11}/_{11}$-1941. — *C.* Left valve of a young specimen c. 1 mm in length, from a breeding aquarium. Helsingør, January 1942. l. ligament, t. teeth.

While hardly any *Tellina* or *Macoma* young occurred in the bottle collectors in the summer of 1941, *Tellina* in all probability occurred in company with *Syndosmya* in the bottle collectors that had been exposed from September 17th to October 22nd, 1939, in which a great many "dirty larvae" had metamorphosed. Unfortunately none of the young were large enough to allow of a definite determination. That the *Tellina* larva occurs in the autumn and winter plankton, appears moreover from the finding of a few bottom stages of *Tellina* sp. in a plankton sample from November 11th, 1941. The largest individual was c. 550 μ long and had a prodissoconch c. 290 μ long (fig. 177 B). In addition it may be mentioned that an aquarium to which several samples with Lamellibranch larvae had been transferred in November-December 1941, in January 1942 contained young, up to c. 1 mm long, bottom stages of *Tellina* sp. (fig. 177 C). The larval type "dirty Lamellibranch larvae" whence these *Tellina* post-larvae were fairly probably derived is seen in fig. 177 A, which was drawn on November 11th, 1941. It is not quite impossible, however, that it is the larva of *Syndosmya*, since according to Kändler's description and drawing this is also egg-shaped. Owing to its egg-shape with the blunt and largest part of the shell in front of the umbos, the veliger shown in fig. 177 A is distinguishable from the more triangular *M. baltica* veliger in its oldest planktonic stages.

Otherwise the two larval types agree fairly well in appearance, having yellowish, rather opaque, dirty shells without especially characteristic features in the internal organisation of the larva. Measurements of prod. I in the larva of *Tellina* sp. are not yet available. (See also the table on p. 311).

Psammobiidae.

Psammobia ferroensis (Chemnitz). Rather rare in the northern part of the Sound. Found southward to Hellebæk.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Egg diameter at Kristineberg c. 160 × 145 μ, that is to say, the same size as in many other Lamellibranchs which are known to have a non-pelagic development.

Solenidae.

Development described by Kändler (1926) (*Cultellus pellucidus*), Lebour (1938 a) (*C. pellucidus* and *Ensis siliqua*), Yoshida (1939) (*Solen gouldi*), and Werner (1939) (*C. pellucidus*).

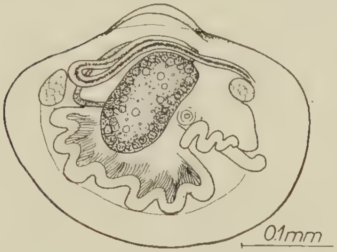


Fig. 178. *Cultellus pellucidus* (Penn.). Veliger c. 325 μ long, from the Sound off Helsingør, $^2/_{12}$-1941.

Cultellus pellucidus (Pennant). Fairly common in the northern part of the Sound. Found down to Taarbæk.

Reproduction: A. Literature. The pelagic larva was first described by Kändler and later by Lebour and Werner, all of whom have published figures of the veliger (see also fig. 178). The species spawns at Plymouth in the autumn and notably in the winter (Lebour). Near Heligoland the veligers were rare as early as November (Kändler). Werner reports prod. I to be 124 μ and the size on metamorphosis c. 345 μ, while Kändler measured the prodissoconch to be 370—380 μ long, which size corresponds to that found in the largest veligers met with in the plankton. The largest individuals found in the plankton at Plymouth were c. 360 μ long (Lebour).

B. Own remarks. Individuals up to 360 μ long were found in the plankton of the Sound. The length of prod. I, measured in ten specimens, varied between 82 and 100 μ (average c. 90 μ).

In the Sound and in southern Kattegat the period of reproduction of *C. pellucidus* is from July to October. During this period the species may be fairly numerous, c. 300 identifiable individuals were counted in a main series on September 5th, 1942. Occasional individuals may, however, be met with at other times of the year. (See also the table on p. 311).

Ensis siliqua (L.). Taken southward to Hellebæk, but rare.

Reproduction: A. Literature. The larva has been described by Lebour. The egg diameter is 70 μ. The oldest veligers may be c. 350 μ long. The veliger much resembles that of *Cultellus*, but has a blunter anterior end. At Plymouth the species spawns in (February), March, and April.

B. Own remarks. The larva was not identified with certainty in the plankton of the Sound.

Mactridae.

Veligers described by Kändler (1926) (*Spisula subtruncata*) and Miyazaki (1936 a) (*Mactra sulcatoria* and *M. veneriformis*).

Spisula subtruncata (da Costa). Very common locally in the northern part of the Sound. Found as far southward as Helsingør.

Reproduction: A. Literature. The species is reported to spawn in the Mediterranean in March-April (Lo Bianco 1899). The larva has been described by Kändler. Near Heligoland the species spawns in autumn and winter (Kändler only observed the larvae in the plankton till December).

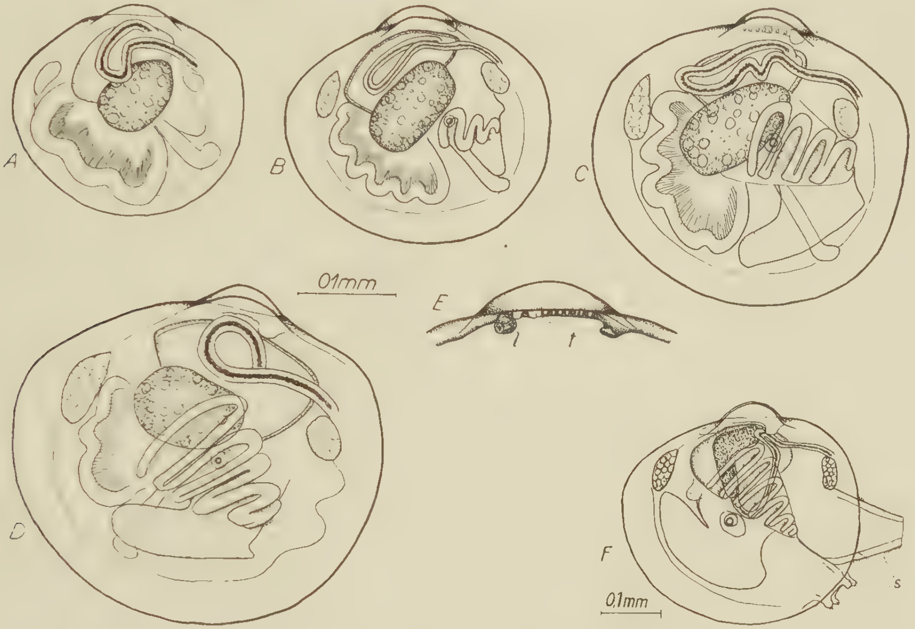


Fig. 179 A-F. *Spisula subtruncata* (Da Costa). — *A.* Veliger c. 240 μ long, from the Sound off Helsingør, $^{10}/_{4}$-1942. — *B.* Veliger c. 280 μ long, from the Sound off Helsingør, $^{2}/_{12}$-1941. — *C.* Veliger c. 330 μ long, from the Sound off Helsingør, $^{2}/_{12}$-1941. — *D.* Veliger c. 375 μ long, from the Sound off Ven, $^{5}/_{6}$-1939. — *E.* Left part of the hinge of a Veliger c. 290 μ long. l. ligament, t. teeth. — *F.* Young post-larva c. 400 μ long, from aquarium, Ven, July 1939. s. siphons.

B. Own remarks. Artificial fertilisation made at Kristineberg in July, but the larvae did not develop beyond the youngest veliger stage. Egg diameter c. 50—55 μ.

It cannot be stated definitely how many of the Lamellibranch larvae found in our plankton samples from the Sound belonged to *S. subtruncata*. As was the case for several other Lamellibranch veligers, the reason is that the range of variation of the specific characters is not yet known, as there may be a possibility for confusion with other veligers whose species have not been determined. Kändler's drawings and descriptions of larvae are, at any rate, insufficient for a certain identification of the species.

A plankton sample which had been kept in an aquarium from July 3rd to 13th, 1939, contained several metamorphosed larvae which agreed entirely in appearance with Kändler's drawing of a young post-larva of *S. subtruncata* (fig. 179 F). The individuals which had metamorphosed in the aquarium had not yet commenced the formation of the dissoconch, but nevertheless they were all about 400 μ long, while Kändler records the length on metamorphosis as 310 μ. Three measurements of prodissoconchs in young of *S. subtruncata* from the Kattegat gave the lengths 320, 350, and 370 μ. Accordingly the size on metamorphosis may, no doubt, be much larger than stated by Kändler; possibly it may be 400 μ or even up to 450 μ, since the veliger which had metamorphosed in our aquaria was found to exhibit these lengths in the plankton. A planktonic individual c. 370 μ long is reproduced in fig. 179 D.

Veligers which fairly certainly belong to the same species as is shown in fig. 179 D may also be met with at other times of the year. They first appear in the plankton in December and reach their maximum occurrence in April-May, when up to several thousand larvae have been present in a main series. In spite of their abundance outside June-July, individuals more than 300—325 μ long are rarely met with at these times, and individuals 400—450 μ long have never been met with outside June-July. Still it is not very probable that we are here concerned with two species. Apart from the difference in the maximum size of the veligers from the summer months and those from the remaining period of their occurrence in the plankton, there is no visible difference between the veligers. And similar variations in the maximum size of the veligers are, in fact, found in several other species, even though, perhaps, it has not been observed previously that the maximum length may be associated with the seasons, as seems to be the case with the larva of *S. subtruncata.* (Similar conditions may, however, possibly be met with in other Lamellibranch veligers, e. g. in *Mytilus edulis.*)

The shell of the veliger of *S. subtruncata* is egg-shaped in outline, with the pointed end anteriorly, but the anterior end may also be fairly blunt. Figs. 179 A—C show different stages of magnitude, figs. 179 A and C representing forms with rather blunt ends, while fig. 179 B shows a more pointed shell. The hinge differentiations, which are more or less distinctly seen in the living larva, may already be observed in individuals c. 200 μ long in the form of a larger number of small irregular teeth. The left hinge of a larva c. 290 μ long is shown in fig. 179 E. The large tooth situated most anteriorly is not found in the right part of the hinge, which is otherwise entirely like the left hinge. Apart from an increase in the breadth of the large tooth anteriorly in the hinge, the differentiation does not proceed further in the plankton even in the largest veligers more than 400 μ long. Thirteen measurements of prod. I gave a mean value of 70 μ (varying between 67 and 77 μ). (Ten measurements were made in the small April individuals, three in large June individuals. There was no difference in the length of prod. I).

The shells of the veligers of *S. subtruncata* are yellowish to yellowish-brown, especially the ventral parts. The areas around the umbos are of a deep purple colour, notably in the larger planktonic larvae. The veliger may resemble the *Cardium fasciatum* veliger fairly much. I. a. the difference in the length of prod. I will no doubt prove to be a suitable character for a distinction of the two species. (See also the table on p. 311).

Spisula solida (L.). Rare in the northern part of the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. The measurement of a single bottom stage showed a prodissoconch length of c. 210 μ. The veliger has not been identified in the plankton of the Sound.

Saxicavidae.

The veligers have been described by Odhner (1914 a) (*Saxicava arctica* and *S. rugosa*), Lebour (1938 a) (*S. arctica* and *S. rugosa*), and Miyazaki (1938 b) (*Hiatella orientalis*).

Panopæa norvegica (Spengler). Fairly common in the northern part of the Sound.
Reproduction: A. Literature. Nothing known.
B. Own remarks. Nothing known.

Arcinella plicata (Montagu). Occurs in the northern part of the Sound.
Reproduction: A. Literature. Nothing known.

B. Own remarks. In October 1939 three young bottom stages which perhaps belong to this species were found in the bottle collectors. The shape and the structure of the hinge much resemble those of *Saxicava*. The right valve was characteristic by having setæ on the posterior dorsal edge (fig. 180 B). The veliger (fig. 180 A), which belongs to the young from the bottle collectors, was found at the same time in the plankton, but was sparsely present (a single or two or three identifiable individuals in a main series). The larva bears a fairly close resemblance to the larva of *Cardium fasciatum*, with which it has possibly previously been confused. (Later on, however, it was probably not present in our plankton samples). The shells are colourless and distinctly concentrically striated. The umbos are of a faint reddish colour. At intense transmitted daylight the whole larva assumes a faint rosy tinge, in contrast to that of *Cardium fasciatum*, which is of a yellowish colour. The umbos are situated fairly near each other, nearer to each other than in the larva of *Cardium fasciatum*. Apart from the ligament, there is no differentiations of the hinge in the pelagic larva. The long straight posterior dorsal line, which, bending rather abruptly, passes into the circular ventral line, is likewise characteristic (fig. 180 A).

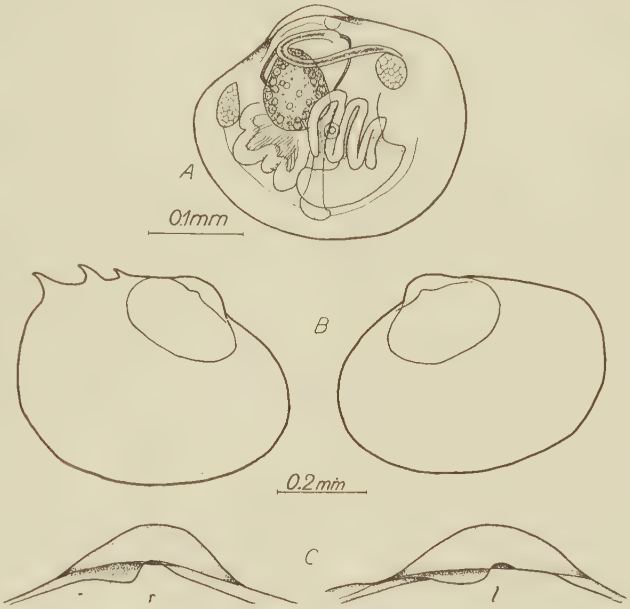


Fig. 180 A-C. *Arcinella plicata* (Mtg.)? — *A*. Veliger c. 280 μ long, from the Sound off Ven, $^{24}/_{10}$-1939. — *B*. The shells of a post-larva c. 650 μ long, from bottle-collectors off Ven, $^{24}/_{10}$-1939. — *C*. The hinge of the same specimen as seen in B. r. right and l. left part of the hinge.

The size on metamorphosis may vary fairly much. The three young bottom stages found in the bottle collectors had prodissoconchs of a length of 245, 280, and 295 μ respectively. A veliger from the plankton measured 280 μ.

Apart from the few veligers taken in October 1939, the larva was not observed in our plankton samples.

Saxicava rugosa Lamarck. Common in the northern part of the Sound.

Reproduction: A. Literature. The veliger has been described by Odhner and Lebour, both of whom record the maximum plankton size as c. 320 μ. The egg diameter is 50 μ. Spawning takes place at Plymouth from the autumn to the early spring (Lebour 1938 a).

B. Own remarks. Prod. I is c. 90 μ long (28 measurements from the Sound and the Little Belt — range of variation from 78 to 98 μ, 15 measurements ranging between 87 and 91 μ).

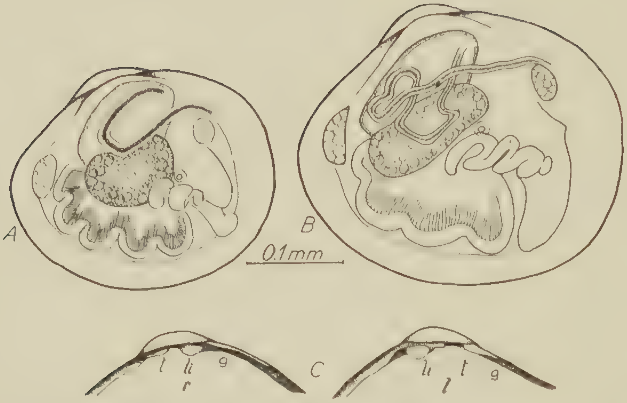


Fig. 181 A-C. *Saxicava rugosa* LAMARCK. — *A*. Veliger c. 280 μ long, and *B*. Veliger c. 340 μ long, both from the Sound off Helsingør, $^{10}/_{4}$-1942. — *C*. The hinge of a veliger c. 375 μ long. r. right and l. left part of the hinge, l. ligament, t. teeth, g. groove.

Having attained a length of 250 μ the veligers are easily recognisable in the plankton (figs. 181 A and B). The larva is long in proportion to its height, and the umbos are situated far forward near the pointed anterior end, while the posterior end is rather abruptly cut off. Moreover the veliger is very thick and will often turn over to the ventral side, so that the umbos are viewed a little from above. The shell is of a yellowish to a deep orange colour, notably on the ventral portions of the shell, and after reaching a length of c. 300 μ the larva is rather opaque. The oldest stages near metamorphosis have often a flesh-coloured mantle edge. The differentiations of the hinge is found in the veliger from a length of c. 300 μ (fig. 181 C). In the right valve a big oblong tooth is developed in the anterior part of the hinge, which fits into a corresponding notch in the left shell. Along the dorsal anterior shell margin of the right valve there is a ridge which fits into a notch in the left valve. This, in its turn, has a ridge along the posterior dorsal shell margin, which engages with a depression in the right valve. In addition there is a well developed ligamental groove. In the Sound veligers more than 350 μ long are fairly common. The prodissoconch of a single bottom stage measured was 375 μ long.

The larva occurs in the plankton of the Sound from April-May to August-September. Off Helsingør a few larvae were seen as early as February. Up to 150 identifiable individuals were found in a main series near Ven and up to 300 near Helsingør. (See also the table on p. 311).

Saxicava arctica (L.). Common in the northern part of the Sound.

Reproduction: A. Literature. The veliger was described by ODHNER (1914a), THORSON (1936), and LEBOUR (1938a). Egg diameter 70—80 μ, largest veligers in East Greenland 390 μ (THORSON). Oldest veligers at Plymouth c. 360 μ long. They occur there from the summer to December (LEBOUR). At Rovigno I myself observed veligers up to c. 360 μ long, still with a well developed velum. ODHNER (1914a) reports the maximum veliger size at Rovigno to be c. 320 μ.

B. Own remarks. Veligers nearly 400 μ long are not rarely met with in the plankton of the Sound. The prodissoconch in two young bottom stages was measured to be 380 and 400 μ long. The veliger is one of the most easily recognisable

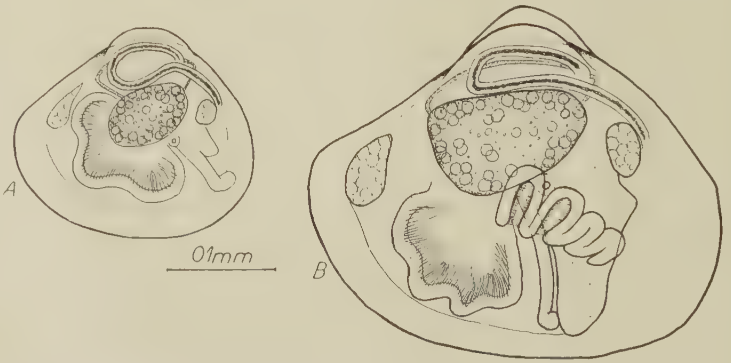


Fig. 182 A-B. *Saxicava arctica* (L.). — *A*. Veliger c. 225 μ long and — *B*. Veliger c. 380 μ long, both from the Sound off Ven, $^{27}/_{8}$-1937.

in the plankton. The typical triangular shape with the anterior end bent slightly upward is assumed already in early planktonic stages (fig. 182 A-B). The veliger is entirely like that of *S. rugosa* in its internal structure and like the latter, it has a flesh-coloured mantle edge in its oldest stages, growing at the same time rather opaque. Prod. I is c. 80 μ long (varying from 70 to 90 μ — 7 measurements). The hinge is entirely like that of the veliger of *S. rugosa.*

The larva of *Saxicava arctica* is commonly met with in the plankton from July to September-November. Up to 100 identifiable individuals were met with in a main series in September (Helsingor). Occasional individuals occur as late as December, January, and February. (See also the table on p. 311.)

Myidae.

Veligers were described by STAFFORD (1912) (*Mya arenaria*) and YOSHIDA (1938) (*Mya arenaria japonica*).

Mya arenaria L. Common throughout the Sound.

Reproduction: A. Literature. Egg size 70—80 μ (BATTLE 1932). The size on metamorphosis is c. 240—300 μ (maximum 320 μ) near Japan, where spawning takes place in May-June (YOSHIDA). Along the east coast of Canada the veliger occurs in the plankton in June-August. The largest individuals are about 300 μ long (STAFFORD).

B. Own remarks. STAFFORD's and YOSHIDA's descriptions are too brief to permit a certain determination of the veliger. The larva (fig. 183) was reared by us in aquarium experiments, and its identity is accordingly indubitable. The shell is fairly circular in outline, but the dorsal lines are almost straight. The umbos are low. Hinge differentiations apart from the ligament do not occur in the plankton stages. Prod. I is c. 95 μ long (varying from 82 to 105 μ, 34 measurements). The shells are colourless, and the larvae are highly transparent. A brownish pigmentation of the soft parts of the somewhat larger, nearly 200 μ long plankton stages will, no doubt, prove to be a reliable specific character. The pigmentation was observed in all the fairly large larvae hitherto examined from our waters (the Sound, Isefjord, the waters off Frederikshavn and near Kristineberg, Sweden). It is especially conspicuous on the velum, but exhibits no definite pattern (fig. 183). (The pigmentation is not mentioned by STAFFORD and YOSHIDA).

The size on metamorphosis is extremely variable. Plankton larvae c. 300 μ long are often met with in the Sound, but the metamorphosis may take place even at a length of c. 200 μ, which is shown by young taken in our bottle collectors. Young bottom stages with a prodissoconch length ranging from 150 to 225 μ are available from the Christianshavn Moat (Copenhagen) (three measurements). In Ringkøbing Fjord the size on metamorphosis in very shallow water (0—30 cm) was c. 210 μ (average of 10 measurements which varied between 200 and 225 μ). In a little deeper water (c. 3 m) the average length of the prodissoconchs was 235 μ (225—250 μ, 5 measurements). In young from a depth of 15—16 m taken off Møen the prodissoconch varied between 225 and 300 μ (ten measurements out of eleven ranged between 270 and 300 μ).

The larva begins to appear in the plankton of the Sound in June and may be met with as late as October. Up to c. 400 identifiable individuals have been counted in a main series (Helsingør, in July), but usually it is not particularly numerous. (See also the table on p. 311).

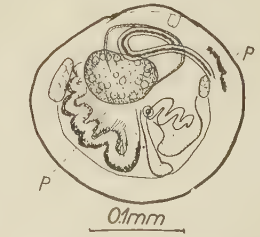


Fig. 183. *Mya arenaria* L. —Veliger c. 220 μ long, from the Sound off Ven, ${}^{10}/_{8}$-1940. p. brown pigment.

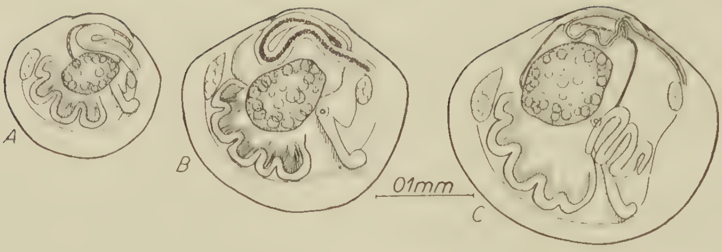


Fig. 184 A-C. *Mya truncata* (L.). — *A.* Veliger c. 155 μ long, — *B.* Veliger c. 235 μ long, and *C.* Veliger c. 280 μ long, all from the Sound off Ven, A. and B. from $^{4}/_{3}$-1939, and C. from $^{29}/_{1}$-1938.

Mya truncata (L.). Common in the Sound. Found southward to Copenhagen.

Reproduction: A. Literature. Egg diameter 70—80 μ in East Greenland (Thorson 1936).

B. Own remarks. A larva very similar to the larva of *M. arenaria* is one of the very few dominant veligers in the plankton in winter. Since numerous very young, up to one millimeter long, bottom stages of *M. truncata* found in April 1942 were taken off Hellebæk at a depth of 30—35 m, we may conclude that the veligers must have occurred in the plankton during the winter and the early spring; for young less than 1 mm long cannot have left the plankton many weeks before. Since, moreover, the prodissoconch of the young agreed closely in shape and size with the biggest of the aforementioned *M. arenaria*-like veligers, it can be regarded as beyond doubt that this veliger actually belongs to *M. truncata*.

The typical *Mya* aspect of the larva is due to the very low and close-set umbos, the lacking differentiation of the hinge (ligament present), the straight anterior and posterior dorsal lines, and the nearly circular line formed by the ventral margin of the shell (fig. 184 A-C). It is distinguishable from the larva of *M. arenaria* by its lack of brown pigment. The shells are faintly yellowish or colourless, and the larvae are very transparent. Prod. I is c. 100 μ long (88—108 μ, 29 measurements). The maximum size of the planktonic larva is c. 320 μ. The length of the prodissoconch in young bottom stages varied between 295 and 340 μ (average c. 315 μ, 13 measurements).

The larva of *Mya truncata* makes its first appearance in the plankton in October. During its maximum occurrence, in November-January, more than 13,000 individuals were counted in a main series (January 1938 off Ven). In February-March it decreases considerably in number, but the larva may be met with as late as April. (See also the table on p. 311).

Corbulidae.

Corbula gibba (Olivi). Fairly common in the Sound.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Egg diameter in the Sound c. 60 μ; the development must accordingly be regarded as pelagic. The length of the prodissoconch in young bottom stages from Nissum Bredning varied between 240 and 255 μ (average 250 μ, 8 measurements).

Owing to the frequency of the adults it might be expected at the outset that the larva of *Corbula* would occur in our plankton samples. And these samples contained, in fact, a larva which in some probability belongs to *Corbula gibba*. This assumption is chiefly based on the characteristic pointed and slightly upward bent anterior end of the prodissoconch observed in young bottom stages and in the veliger. The outline of the prodissoconch agrees entirely with that of the oldest veligers occurring in the plankton. Moreover the length of the prodissoconch agrees with the maximum length of the planktonic veliger, which is c. 250 μ.

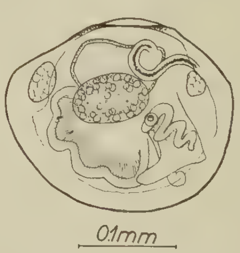


Fig. 185. *Corbula gibba* (Olivi)? — Veliger c. 235 μ long, from the Sound off Helsingør, $^{17}/_{9}$-1941.

The supposed *Corbula gibba* veliger (fig. 185) is a very thick larva, which can hardly lie on the side without turning over to the ventral side. It is colourless and transparent. (The prodissoconch of the *Corbula* young examined was likewise colourless. Yellowish prodissoconchs are most frequently met with in other Lamellibranchs). The umbos are low and situated far apart. No hinge differentiations occur in the planktonic larva, but the dorsal shell margins in front of and behind the umbos are very vigorous.

The larva was not registered near Ven. However, it may easily have been overlooked. Off Helsingør it was encountered regularly in September-October (up to c. 30 identifiable individuals in a main series). In addition it was collected on a few occasions in winter and spring. (See also the table on p. 311).

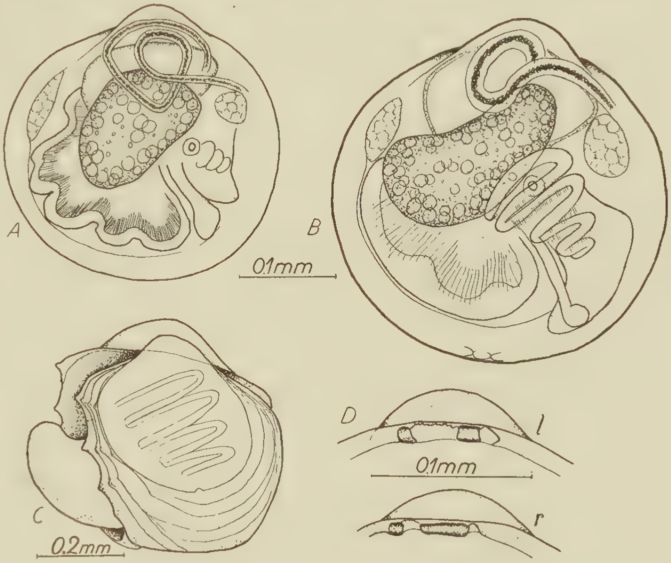


Fig. 186 A-D. *Zirphæa crispata* (L.). — *A*. Veliger c. 285 μ long, from the Sound off Ven, $^{29}/_{1}$-1939. — *B*. Veliger c. 340 μ long, from the Sound off Ven, $^{1}/_{7}$-1939. — *C*. Post-larva from bottle-collectors off Ven, $^{13}/_{8}$-1940. — *D*. Hinge of an older veliger, l. left and r. right part of the hinge.

Pholadidae.

Veligers have been described by Kändler (1926) (*Pholas* sp.), Miyazaki (1936a) (*Parapholas quadrizonata*), Lebour (1938a) (*Barnea parva* and *Pholadidea loscombiana*), and Werner (1939) (*Zirphæa crispata*).

Zirphæa crispata (L.). Common in the northern part of the Sound.

Reproduction: A. Literature. Egg size 40 μ (Griffin (1899), the Pacific coast of the United States). Werner has described the veliger from Heligoland. Prod. I is 93 μ long. The full-grown veliger is 306 μ long and 300 μ high. Bouchard-Chantereaux (1879) observed the ejection of veligers from the mantle cavity of the adults near Boulonnais in the months June-September. At their birth the larvae were only a little over 100 μ long.

B. Own remarks. Measurements of prod. I from the Sound and the Little Belt showed an average length of c. 85 μ (range of variation 76—92 μ, 17 measurements). The veligers are readily recognisable in the plankton right back to the very young stages on account of their circular shells (fig. 186A). The shells are yellowish and transparent in the young larvae, but on attaining a length of about 300 μ the larva grows darker and rather opaque. From this length the larvae have likewise often a flesh-coloured mantle edge. The area around the umbos are distinctly purple-coloured. Hinge differentiations occur already in veligers c. 200 μ long. Two big teeth are formed in each half of the hinge (fig. 186D). Before metamorphosis an articular connection is found on the ventral side, where a knob on the right shell margin engages with a notch in the left shell margin (fig. 186B). In the Sound the veligers seem in most cases to be about 340—350 μ long before leaving the plankton (fig. 186B). The prodissoconch of a single bottom stage derived from the bottle collectors was 360 μ long (fig. 186C).

The veliger of *Zirphæa crispata* is found in the plankton throughout the greater part of the year. Its frequency maxima are not associated with any particular season. They occurred in June and November 1938, September 1939, and September and November 1941. But minor spawnings may set in in the winter or spring also. (See also the table on p. 311).

Pholas candida L. Occurs in southern Kattegat.

Reproduction: A. Literature. According to Bouchard-Chantereaux (1879) it would seem that this species, like *Zirphæa crispata*, spawns the veligers, which are only slightly more than 100 μ long, in the months June-September. The veligers have not been described before.

B. Own remarks. Our plankton samples occasionally contained a few individuals of a veliger of entirely the same type as the *Zirphæa crispata* veliger, but of a different and very characteristic shape, the shell outline being square (fig. 187), often with a more or less marked indentation in the ventral side. All the individuals observed had apparently almost reached the size at which they metamorphose—being from c. 330 to c. 370 μ long. It was impossible to trace the species back to younger planktonic stages. The hinge is indistinguishable from that of *Zirphæa*, and the colour, transparency, and internal structure likewise agree in the two larvae. Hence there can be little doubt that we are here concerned with the veliger of the other Pholadid occurring in the inner Danish waters, viz. *Pholas candida*. The reason why only individuals ready to metamorphose have been met with, is no doubt that the species does not live in the immediate neighbourhood of the Sound (in any great numbers), so that most veligers attain a large size while they drift with the current down towards the Sound.

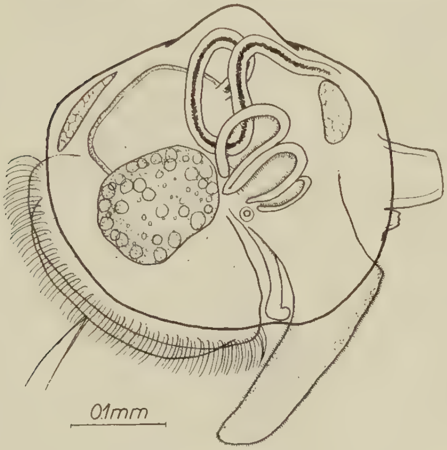


Fig. 187. *Pholas candida* L.?—Veliger c. 370 μ long, from the Sound off Ven, $^{8}/_{10}$-1938.

The *Pholas candida* veliger was found in the months July-November, but always only one single or some few at a time, and similarly they were not met with in each main series during their period of occurrence. (See also the table on p. 311).

Xylophaga dorsalis Turton. Only found on a very few occasions in the Sound and in other Danish waters.

Reproduction: A. Literature. Nothing known.

B. Own remarks. No veliger that might be assumed to belong to this species occurred in the plankton of the Sound.

Teredinidae.

Veligers have been described by de Quatrefages (1849) (*Teredo* sp.), Hatschek (1881) (*Teredo* sp.), Sigerfoos (1895) (*Teredo megotara* and *T. navalis*?) and (1908) (*Xylotrya gouldi*), Miyazaki (1935) (*Teredo japonica*), and Lebour (1938a) (*Teredo norvegica* and *T.* sp.).

Teredo megotara Hanley. The species is reported to have been found near Copenhagen.

Reproduction: A. Literature. The species spawned in the summer at the marine laboratory at Beaufort. The eggs are fertilised in the water. The larva has only been followed to the Trochophora stage (Sigerfoos 1895). In our waters spawning may take place during the greater part of the year. Here, also, the sexual products are spawned freely in the water (Kramp 1937).

B. Own remarks. Two individuals of a Teredinid—recognisable by the three teeth in the right hinge (fig. 188 B), in contrast to the *Pholadidae*, which have only two teeth—which with a fairly great probability may be regarded as *T. megotara*, were found in the plankton off Helsingor. The only other possibility is *T. norvegica*. However, this form is much rarer in the Danish waters than *T. megotara*, which is dominant and very numerous near Hirtshals (Kramp 1937), while it is much less frequent inside the Skaw.

The veliger of *T. megotara* has almost circular shells (fig. 188 A), but in regard to habit it is distinguishable from *Zirphæa* by its greater opacity even in the young planktonic stages. The opacity is probably mainly due to the shells, which are of a dark yellowish-brown colour. The conspicuous umbos and the area around them are reddish-brown, while the mantle edge of the individuals observed was flesh-coloured. The muscular attachments were oblong and were of a distinctly lighter colour than the remaining parts of the larva. Both the velum and the foot were well developed in the individual drawn, which had not yet reached the size at which it metamorphoses. Plankton samples from Hirtshals (kindly handed over to me by Dr. P. L. Kramp) with veligers of *T. megotara* contained individuals measuring up to c. 330 μ in length. The prodissoconch of post-larval stages almost without any development of the dissoconch, derived from the same place, were on an average 345 μ high (319—363 μ, 9 measurements) and 335 μ long (323—352 μ, 6 measurements).

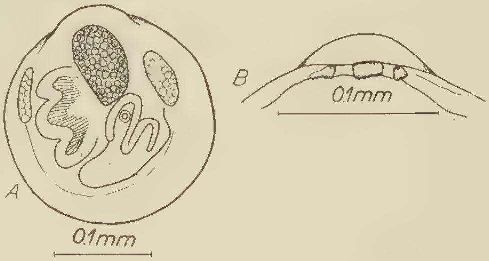


Fig. 188 A-B. *Teredo megotara* Hanley?—*A*. Veliger c. 220-30 μ in diameter, from the Sound off Helsingør, $^2/_{12}$-1941.—*B*. The right part of the hinge from the same specimen as seen in A.

Of the two individuals hitherto found, one occurred in the samples in December 1941, the other in July 1942 (both off Helsingør).

Teredo norvegica Spengler. The species hardly occurs in the Sound in fixed timber.

Reproduction: A. Literature. The veliger has been described by Lebour. The species spawns at Plymouth all the year round. The eggs are fertilised in the water. Egg diameter 40 μ. The oldest veligers in the plankton may be c. 380 μ long, and are almost circular. Some veligers, no doubt of this species, were observed to have a black eye spot.

B. Own remarks. Our plankton samples contained no veliger which might be assumed to belong to *T. norvegica* (cf. also the remarks under *T. megotara*).

Teredo navalis L. Common throughout the Sound.

Reproduction: A. Literature. The free planktonic stages have not been described before.

B. Own remarks. The veliger of *T. navalis* was identified by comparisons of the prodissoconch with that of very young burrowing stages from Kristineberg and the harbour of Helsingør, while the youngest stages were dissected out of sexually mature individuals derived from the Little Belt.

Egg diameter 55—60 μ. The largest larvae, found in adult sexually mature animals from the Little Belt, were c. 80 μ long. In one individual the average length of the larvae found was c. 80 μ (range of variation 70—83 μ, 23 measurements), in another individual c. 82 μ (range of variation 80–86 μ, 10 measurements). Altogether eight females in function were examined, but in no case were veligers found in a more advanced stage than those mentioned above, and in no case had the development of the final prodissoconch commenced. As the individuals were examined far into the spawning period of the species (July 28th — numerous veligers were met with in the plankton at any rate two weeks before this date), it might be expected that the larvae are spawned when they have reached a length of c. 80 μ, and that this length corresponds fairly closely to the length of prod. I. At the same time, however, veligers of a length down to c. 70 μ were met with in the plankton; they had already commenced the formation of the final prodissoconch, which was easily recognisable by its flaxen colour. Moreover these larvae had already incipient hinge teeth. Even in the largest veligers, dissected out directly of the adults, there were no indications of hinge differentiations. Measurements of prod. I in planktonic veligers (July 16th) gave 72 μ on an average (range of variation 65–80 μ, 16 measurements). It is worth noticing that in larvae derived from the same mother individual prod. I evidently varies much less in size than in an assemblage of veligers derived from different mother animals, as may be met with in the plankton. This means a considerable reduction in the reliability of prod. I as a specific character (see also p. 279).

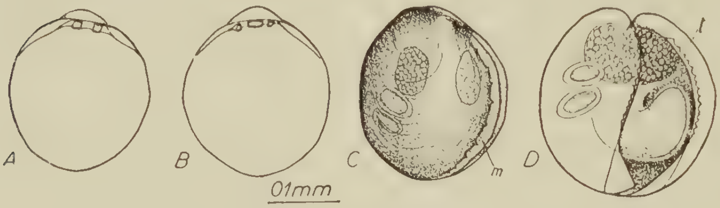


Fig. 189 A-D. *Teredo navalis* L. — *A.* The left valve and *B.* The right valve of a veliger c. 210 μ long showing the structure of the hinge. — *C.* Veliger and *D.* Young post-larva from Gullmarfjord, Sweden, July 1939. m. mantle edge, t. serrated ridge.

While in the Danish waters the veligers are spawned when they are c. 70—80 μ high, near Rovigno they remain in the mother individual till they are c. 260 μ high, that is to say, till they are ready to metamorphose.

The young veligers are circular, but later on they especially grow in height, the somewhat larger larvae being much higher than long (fig. 189). The veligers are easily recognisable in the plankton owing to the strongly flaxen-coloured shells of the young individuals and the yellowish-brown to greyish-brown colour of the shell and the greater opacity found in the somewhat older larvae (fig. 189C). The umbos are conspicuous and of a deep purple colour. Like other Teredinids the larva is very thick in its older stages, so that it may hardly lie on the side. The larval hinge consists of two equally large teeth in the left and three teeth in the right valve, of which the midmost one is the largest (fig. 189 A-B). Veligers ready to metamorphose are c. 250 μ high. (A corresponding size was found for the prodissoconch of young bottom stages and for the largest veligers in the plankton.) Immediately after passing into the burrowing stage, the anterior margins of the shells are provided each with its serrated ridge, and an articular connection is developed on the ventral side of the shells (fig. 189D).

The veliger of *Teredo navalis* was never numerous in the plankton of the Sound, the number of individuals found in a main series not exceeding ten. The larva mainly occurs in summer and autumn. Outside this period it was only observed once, viz. in January 1939. (See also the table on p. 311).

Thraciidae.

Thracia papyracea Poli. Occurs southward to Hellebæk.

Reproduction: A. Literature. Nothing known.

B. Own remarks. Nothing known.

Table showing the occurrence of larval Lamellibranchs in the Sound plankton off Helsingør, depth 30—0 m, from September 1941 to September 1942 (for explanation see the text pp. 279—280).

Species	1941				1942								
	September	October	November	December	January	February	March	April	May	June	July	August	September
Anomia squamula	×	× ×	× ×	×	×	. .	. .	×	. .	. .	×	× ×	× ×
Pecten septemradiatus	× ×	× ×	×	. .	. .	. .	. .	. .	. .	. .	×	. .	. .
— *opercularis*	×	×	. .	. .	. .	. .	. .	. .	. .	. .	×	×	. .
— *striatus*	×	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	×
Lima loscombi	× ×	× ×	× ×	. .	. .	. .	. .	. .	. .	. .	. .	. .	× ×
Mytilus edulis	× × ×	× ×	×	× ×	× ×	×	×	. .	. .	× × × × ×	× × × × ×	× × × × ×	× × ×
Modiolaria marmorata	× ×	×	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
Montacuta bidentata	× × ×	× × ×	× ×	. .	×	. .	. .	. .	. .	. .	× × ×	× × ×	× × ×
— *ferruginosa*	× ×	× ×	. .	. .	. .	. .	. .	. .	. .	. .	× ×	×	× ×
Cardium fasciatum	× × ×	× ×	×	. .	. .	. .	. .	. .	. .	. .	×	× ×	× × ×
— *edule*	×	×	. .	. .	. .	. .	. .	. .	. .	× ×	× × ×	× ×	. .
Venus gallina	×	× × ×	× × ×	× ×	× ×	×	. .	. .	. .	. .	. .	× ×	× ×
Tellinidæ and *Semelidæ* (see p. 297-300)	×	× × ×	× × ×	× ×	× ×	. .	. .	. .	× × ×	× × ×	× × ×	× × ×	× × × ×
Cultellus pellucidus	× × ×	× ×	×	×	×	×	. .	. .	. .	. .	× ×	× × ×	× × ×
Spisula subtruncata	(×)	. .	. .	× ×	× × ×	× ×	×	× × × × ×	× × ×	× × × ×	× ×	. .	. .
Saxicava rugosa	. .	. .	. .	. .	. .	×	. .	× ×	×	× ×	× × ×	. .	. .
— *arctica*	× ×	× ×	× ×	×	×	. .	. .	. .	. .	. .	× ×	×	× ×
Mya arenaria	×	×	. .	. .	. .	. .	. .	. .	. .	× × ×	× × ×	×	. .
— *truncata*	. .	× × ×	× × × × ×	× × × × ×	× × × × ×	× ×	× ×	× × ×	. .	. .	. .	. .	. .
Corbula gibba	×	× ×	. .	×	×	. .	. .	×	. .	×	× ×	. .	× ×
Zirphæa crispata	× × ×	× ×	× × × ×	× ×	× ×	× ×	. .	. .	. .	× ×	× × ×	× × ×	× × × ×
Pholas candida	×	×	×	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
Teredo navalis	×	×	×	. .	. .	. .	. .	. .	. .	. .	×	. .	×
Small indeterminable larvae	× × ×	× × ×	× × × × ×	× ×	× × × ×	× × ×	×	×	× ×	× × × ×	× × ×	× × × ×	× × ×

10. Cephalopoda.

Up to the present day fourteen species of *Cephalopoda* have been recorded from the area the Skaw–Bohuslän the Belts and from the Baltic, viz. *Eledone cirrosa, Bathypolypus arcticus, Sepietta oweniana, Sepiola atlantica, Rossia glaucopis, Rossia macrosoma, Sepia officinalis, Loligo vulgaris, Loligo forbesi, Alloteuthis subulata, Onychoteuthis banksi, Architeuthis monachus, Todaropsis eblanae,* and *Ommatostrephes sagittatus* (cf. Aurivillius 1898a, Grimpe 1925, 1933, Lenz 1873, Lovén 1846, 1847a, b, and 1848a, Lönnberg 1891, Malm 1863, Pfeffer 1808, Posselt 1889, Spärck 1928, Steenstrup 1849, 1850, 1855, 1884, and 1900, and Ellen Thomsen 1934). Five of these species are recorded from the Sound, viz. *Sepietta oweniana, Rossia macrosoma, Loligo forbesi, Onychoteuthis banksi,* and *Architeuthis monachus* (cf. Grimpe 1925, Lönnberg 1891, Posselt 1889, Spärck 1928, and Steenstrup 1855), to which may be added the unpublished finds of *Eledone cirrosa* and *Alloteuthis subulata,* and the eggs of *Loligo vulgaris* (see below). Thus reliable records of eight species of Cephalopods are known from the Sound.

Eledone cirrosa Lamarck. During recent years about 25 spms. of *Eledone sp.* have been taken in deep water within the area Gilleleje—Kullen near the northern mouth of the Sound (kind information from the teacher in Gilleleje, Mr. H. C. Terslin). As *Eledone moschata* is absent from our waters (cf. Grimpe 1925) and as the present author has examined a typical *Eledone cirrosa* taken off Ellekilde Hage, depth 20 m, in the spring of 1942, the identity seems to be certain.

Reproduction. A. Literature. Hertling (1936) describes and figures egg clusters spawned in the Heligoland laboratory on $^{4}/_{10}$-1935. The club-shaped, whitish, transparent capsules (about 8 mm long and 3 mm in largest breadth) continue rather gradually into a thin string, by which the capsule adheres near the base of other capsules to a common substratum. The embryos are yellowish, but no further details are given.

B. Own remarks. No observations are available from the Sound. — In the Malmö museum (Sweden) is found an egg-mass of this species taken S.W. of Måseskär (Bohuslän, Swedish W.coast), depth ?, on $^{11}/_{7}$-1938 (kind information by Mr. P.-M. Lovén).

Sepietta oweniana (Orb.) Pffr. Known from Helsingor (1 ♀), and from Gilleleje (1 ♀) (Posselt 1889, p. 141). Further, from the Kattegat (i. a. Frederikshavn), and Bohuslän.

Reproduction. A. Literature. Naef (1921, p. 648) mentions and figures (text-fig. 381 a—b) young just hatched from the egg-mass, but he gives no figures or descriptions of the eggs, which—as far as I know—are still undescribed. — Jatta (1896) figures various egg-masses of other species of Sepiolids.

B. Own remarks. The collections of the Copenhagen museum include an egg-mass (fig. 190 A) taken off Nordre Rønner in northern Kattegat, depth 8 m, on $^{10}/_{8}$-1927, which seems to belong to this species. The old embryos found in the eggs (fig. 190 C—D) showed a very close similarity to the embryos of this species figured by Naef (1921, p. 648, fig. 381 a—b). Thus it could be taken for granted that the eggs belonged to the *Sepiola-Sepietta*-type. Only two species of this group occur in our waters inside the Skaw, viz. *Sepiola atlantica* and *Sepietta oweniana*; the latter has been taken on several occasions while the former seems to be rare. As, further, the egg-mass of *Sepiola atlantica* described by Grimpe (1925, p. 18) from Heligoland (where this species is common and *Sepietta oweniana* rare) could be excluded owing to

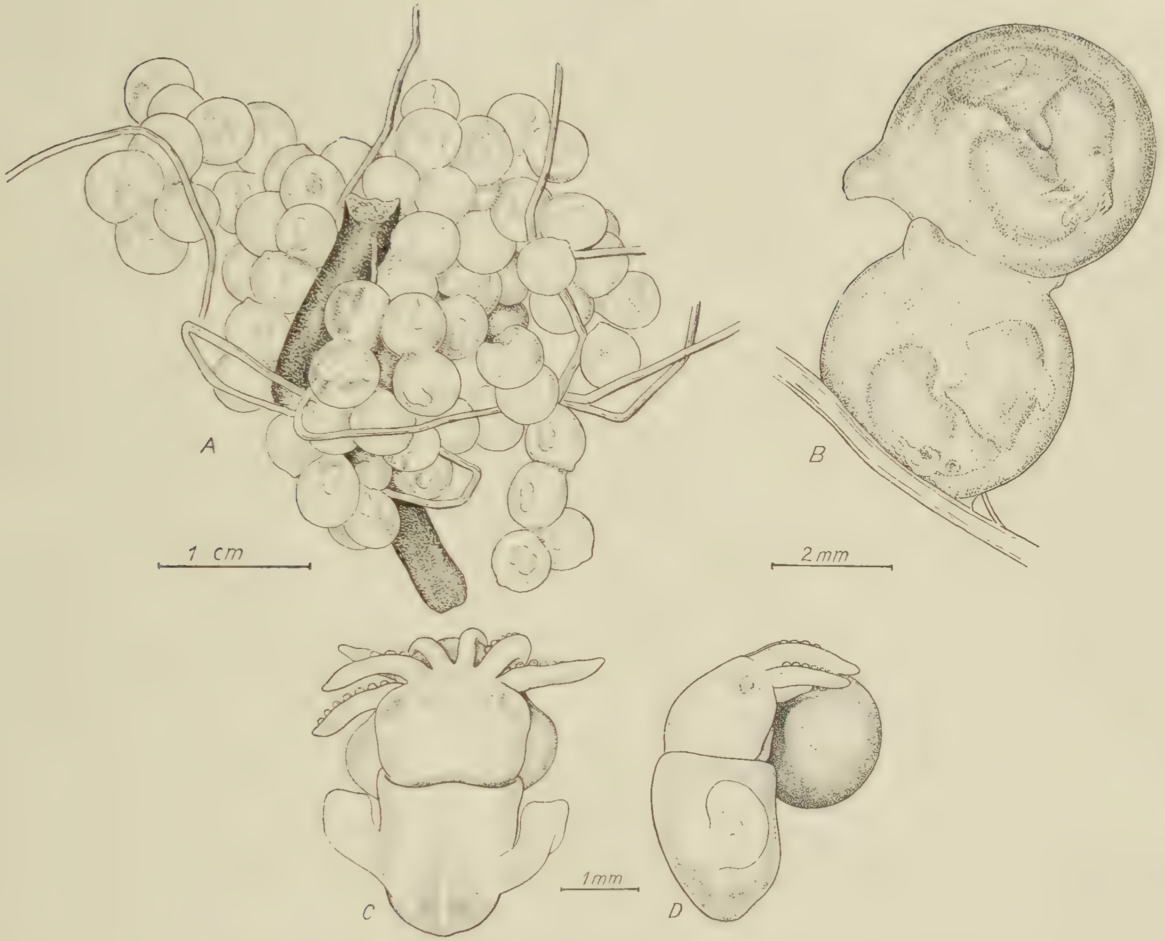


Fig. 190 A-D. *Sepietta oweniana* (Orb.) Pffr. — Egg mass taken off Nordre Rønner, N. Kattegat, depth 8 m, on $^{10}/_{8}$-1927. Drawn from material preserved in alcohol in the Copenhagen museum. — *A*. The egg mass *in situ* on a piece of sea-weed. 2 × natural size. — *B*. Two eggs with the embryos visible through the shell. — *C* to *D*. Embryos dissected out of the eggs. A large yolk-sac is still present. Seen from the dorsal side (C) and the right side (D). (Drawn by Poul H. Winther).

its small egg size (2.5 × 3.5 mm only), and as Grimpe (l. c.) suggests the eggs of *Sepietta oweniana* to be much larger, it seems reasonable to refer our egg-mass to *Sepietta oweniana*.

This egg-mass (fig. 190 A—B) consists of about 130 spherical to lemon-shaped, transparent, colourless-brownish eggs (4.3—4.4 × 4.9—5.2 mm) attached to a piece of sea-weed and surrounded by algal filaments. In contrast to the *Rossia* capsules, which have tough, untransparent egg membranes, the *Sepietta* capsules have very thin membranes. Where the capsules join each other or adhere to a substratum, they are somewhat flattened and connected by thin brims, and a bud like that at the top of a lemon is found at the distal end of each capsule.

The embryos (fig. 190 C—D) show the same stage of development in all the capsules; they have already developed the characteristics of the adults, although a yolk sac is still present.

The breeding of this species in Danish waters has hitherto been unknown.

Rossia macrosoma (DELLE CHIAJE). Records are available from the area Hornbæk—Gilleleje—Höganäs (POSSELT 1889, and kind information from Mr. TERSLIN, Gilleleje).

Reproduction. A. Literature. The eggs are described and mentioned by GRIMPE (1925, pp. 24—27, pl. fig. 6), JATTA (1896, p. 139), LÖNNBERG (1891), NORDGAARD (1922, fig.), POSSELT (1889), and STEENSTRUP (1850, 1900, fine figures). The individual eggs—7.8 to 9 mm across including the egg membrane—are nearly spherical, protruded at their distal end into a small bud like that of the distal end of an incandescent lamp; they are purplish-brown and attached to each other and to the substratum by thin brim-like membranes. Where two eggs join each other, their outer membranes are flattened, and the eggs adhere so much to each other that they are difficult to separate without hurting them. The closely related *Rossia glaucopis* has smaller eggs (about 7 mm across including the membranes) with a yellowish-white surface, and are thus easily distinguished from those of *Rossia macrosoma*. Further the old embryos of the latter species have several rows of small suckers along the arms, while old embryos of *R. glaucopis* have only two rows of large suckers along each arm. STEENSTRUP (1900, pl. fig. 16) gives an exceedingly characteristic figure of the egg-mass of *R. macrosoma* from the Kattegat. — Sponges, shells of large Lamellibranchs, and stones are used as substrata. — In the North Sea egg-masses are found from late June to the middle of September.

B. Own remarks. Five egg-masses of this species from the waters inside the Skaw are found in the collections of the Copenhagen museum, viz., three from the Sound and two from other areas:—

1. Off Gilleleje, date and depth unknown, one egg-mass with about 20 eggs, five of which measured 9.1 × 10.5—9.2 × 11.7—9.8 × 11.1—10.0 × 11.8, and 10.2 × 10.4 mm respectively. All the eggs contained large embryos with a small yolk-sac, and the arms bore several rows of small suckers as characteristic of *R. macrosoma*.

2. Gilleleje Flak, depth about 32 m, $^{25}/_{1}$-1934, one egg-mass with about 50 newly spawned eggs attached to the inner surface of an old cup. Five of them measured 9.9 × 12.7—10.0 × 12.7—10.0 × 13.2—10.2 × 11.9, and 10.3 × 13.4 mm respectively. All the eggs were in the same stage of development, and they all seem to originate from a single spawning of a single female.

3. Ten miles NW. to W. of Kullen, depth 32 m, $^{29}/_{10}$-1904, one egg-mass with about 20 eggs fixed to a piece of cinders. Four of the eggs measured 9.4 × 10.4—9.5 × 10.2—9.2 × 9.6, and 8.7 × 11.3 mm respectively. They all contained embryos 3 to 4 mm long with a yolk-sac 4 mm across.

4. SE. of Anholt lightship, depth 40 m, $^{17}/_{6}$-1901, one egg-mass with about 30 eggs, two of which measured 9.3 × 11.8 and 9.9 × 10.8 mm respectively. Substratum unknown. The eggs were poorly preserved and the stage of embryonic development could not be ascertained.

5. North of Marstrand (Bohuslän, Swedish W. coast), depth 90 to 130 m, taken on $^{4}/_{8}$-1911, one egg-mass with about 30 eggs, all of which contained young embryos. Three eggs measured 9.9 × 11.3—10.9 × 12.0, and 11.1 × 12.0 mm respectively. Substratum unknown.

Rossia macrosoma seems thus to breed regularly in our waters, and breeding seems to take place throughout the year.

Loligo forbesi STEENSTRUP. The species has been recorded from Helsingor (POSSELT 1889) and Gilleleje (SPÄRCK 1928). Mr. TERSLIN has kindly informed me that about 30 spms. of *Loligo*, presumably belonging to this species, have been caught within the area Gilleleje-Kullen in recent years.

Reproduction. A. Literature. Lo Bianco (1909, p. 648) briefly mentions the egg-mass, but the first thorough description and figure are given by Grimpe (1925, p. 36, pl. fig. 8b). The egg-mass described and figured by Lönnberg & Gustafson (1934) from the Gullmarfjord belongs to *Loligo vulgaris* (see below).—The nearly spherical, dark-yellowish eggs—4.1 × 3.9 mm —are embedded in colourless, transparent and gelatinous envelopes shaped like a torpedo or a cigar. Each envelope—from 67 to 165 mm long and 10 to 12 mm broad—contains on an average about 50 eggs (minimum 31, maximum 61) and several envelopes are attached to a common base by thin, short, gelatinous strings. At least 11, probably much more, envelopes are contained in a single spawn. The hatching young are of the shape of the adults. Egg-masses were found in the North Sea in late July, October, and early November. The species is thus a typical autumn breeder, and seems to live for more than one year.

B. Own remarks. No egg-masses of those mentioned by Posselt (1889, p. 143) were to be found in the collections of the Copenhagen museum, which, however, contained two other egg-masses of this species, both from the North Sea:

1. North of Hanstholm, depth 33 m, on $^{26}/_{9}$-1930. About 40 envelopes; at least 7 of these were fastened to a common base. Five envelopes (preserved in formalin) measured 101 × 14—104 × 14—109 × 13—111 × 14, and 125 × 14 mm, and contained 43—59—68—73, and 79 eggs or embryos respectively. Some of the envelopes contained newly laid eggs, others young embryos, and others again embryos ready to hatch.

2. The North Sea, depth ?, July 1935, two envelopes each about 75 × 10 mm, and with about 50 eggs.

Thus at present we have no finalproof that this species breeds in the waters inside the Skaw.

Loligo vulgaris Lamarck. Hitherto unknown from the Sound, but recorded from Bohuslän, the Limfjord, Kattegat, and the western Baltic (cf. Posselt 1889, Grimpe 1925).

Reproduction. A. Literature. The egg-masses are described or mentioned by Bohadsch (1761, p. 150, pl. 12), Grimpe (1925, pp. 35-37, pl. fig. 8a), Herklotz (1859, pp. 12—15, fig. 1, pl. 1, figs. 4—5), Hoek (1893, p. 64), Jatta (1896, pl. 7, fig. 1 as *Loligo forbesi*), Lönnberg & Gustafson (1934, fig. 1, as *Loligo forbesi*), and Nozeman (1757, p. 379). Grimpe (l. c.) gives the results of a detailed study of them, and Tinbergen & Verwey (1945) give some data on the reproduction. Males and females are sexually ripe when about one year old, e. g. 13—14 cm long. During the following year the growth of male specimens far exceeds that of female specimens, probably because the latter use a large part of their surplus to produce their eggs (Tinbergen & Verwey 1945). The ripe animals migrate to the coastal waters to spawn there in May (main-spawning) to August. The female spawns more than one egg-mass, the first spawn being the larger one. The eggs shaped like a hen's egg—3.5 × 3.1 mm are embedded in whitish-colourless, opaque, gelatinous envelopes shaped like a torpedo or a cigar. Each envelope—about 100 to 120 mm long and 10.8 to 12.5 mm thick—contains on an average 100 to 120 eggs (Grimpe). A single spawn may contain about 50 envelopes attached to a common base (Lönnberg & Gustafson 1934), but several females may deposit their spawn together. A single female may be estimated to spawn up to 4000 or 5000 eggs. The whitish colour and the opacity of the envelopes, the large number of eggs, and the shape and smaller size of the eggs make this spawn easily distinguishable from those of *Loligo forbesi* (see above). The hatching young are of the shape of the adults. Egg-masses have been taken in the North Sea in May, June, and July, and the species is thus a spring- and summer-breeder (*L. forbesi* breeds in late summer and autumn, Grimpe).

B. Own remarks. An egg-mass in the Copenhagen museum, taken 7 miles N.W. of Gilleleje, depth 21 m, on $^{5}/_{3}$-1931, proved to belong to this species. It consisted of 13 envelopes of the common whitish-opaque type (preserved in formalin) and attached to a common base. Two envelopes measured 94 × 14 and 96 × 14 mm respectively, and five envelopes contained 113—130—142—145, and 161 eggs respectively in the first stages of development.—This egg-mass agrees on all points with the description of Grimpe (1925). It is interesting that our egg-mass as well as that described by Lönnberg & Gustafson (l. c.) from the Gullmarfjord were taken in March, i. e. earlier in the spring than the finds from the North Sea. These two finds show—in contrast to Grimpe's supposition—that the species is a native of our waters and is able to breed there. The egg-mass from Gilleleje is the first find of this species from the Sound.

Alloteuthis subulata (Lamarck). Mr. Terslin, Gilleleje, has kindly informed me that this species has on certain occasions been taken in large numbers in hauls with sprat-trawls in the area Gilleleje Flak—Kullen (at the northern entrance of the Sound) in recent years. The species is further recorded from Bohuslän, the Kattegat, the Limfjord, and the western Baltic.

Reproduction: A. Literature. The spawn was described by van Beneden (1841, pp. 1—11, as *Sepiola*) and by Grimpe (1925, p. 60, pp. 63—66, text-fig. 24, and pl.fig. 14). Further Spärck (1928) has seen the eggs in the western Limfjord. The eggs, to a number of 28—30 (minimum 19, maximum 55), are embedded in quite transparent, club- to pear-shaped envelopes of a very thin mucus. The envelopes are 24 to 28 mm long (40 mm when the stalk is included), and 7 to 9 mm in largest diameter. Several envelopes are united by their stalks to a common cluster attached to a substratum (hydroids, stones, etc.). A single female may deposit up to 30 to 45 envelopes, i. e. 1000 to 1500 eggs, but several females may deposit their eggs in a common cluster. This species is only annual. Some specimens spawn in the spring, others in the autumn. In the Limfjord egg-masses have been observed about the middle of July. The hatching young are of the shape of the adults.

B. Own remarks. No observations are available from the Sound, but in the collections of the Copenhagen museum the following egg-masses were found:

1. N. of Læsø (Northern Kattegat), depth 21—23 m, taken on $^{30}/_{7}$-1898. One egg-cluster with about 60 envelopes in two different stages of development (young embryos, and embryos nearly ready to hatch). Five envelopes contained 24—31—33—34, and 36 eggs or embryos respectively.

2. Off Hjellen at Frederikshavn, NW. Kattegat, depth ?, $^{29}/_{7}$-1935. One large cluster consisting of about 100 envelopes with rather large embryos. Five envelopes contained 27—29—29—31, and 35 embryos respectively.

3. Off Frederikshavn, NW. Kattegat, depth ?, $^{1}/_{8}$ to $^{16}/_{8}$-1935. One cluster consisting of 15 envelopes with large embryos. Five envelopes contained 29—33—35—37, and 37 embryos respectively.

4. Nissum Bredning, the Limfjord, depth 6 m, $^{16}/_{7}$-1927 (cf. Spärck 1928). One cluster with about 50 and one with about 15 eggs and large embryos respectively. Two envelopes with newly laid eggs contained 29 and 37 eggs respectively, and three envelopes with embryos contained a number of 35—39, and 51 respectively.

5. Horns Rev area, the North Sea, depth ?, on $^{10}/_{6}$-1904. One cluster of about 25 envelopes and one of about 35 envelopes, both containing newly laid eggs. Five envelopes contained 22—22—25—26 and 39 eggs respectively.

6. Horns Rev area, the North Sea, depth ?, June 1936. Several hundreds of envelopes in large clusters and in all stages of development. An envelope 31 × 9 mm (including the stalk) contained 41 eggs, another 27 × 12 mm contained 34 eggs, a third 26 × 9 mm 48, a fourth 24 × 10 mm 36, and a fifth 24 × 7 mm 51 eggs.

The main spawning seems thus to take place in the actual summer, at any rate in the inner Danish waters.

Onychoteuthis banksi (Leach). One specimen known from the Sound (Posselt 1889, p. 144). Further records from the Kattegat (one spm.) and from Bohuslän (a few spms.).

Reproduction: Unknown.

Architeuthis monachus Steenstrup. Old records from the Sound off Malmö (Steenstrup 1855, Lönnberg 1891). Not found later.

Reproduction: Unknown.

II. Crustacea.

A. Cirripedia.

During our investigations in the Sound this group has only been treated in very broad features. The significance of Cirriped larvae in the Sound plankton is only small as compared with the numbers of larvae of most other groups of bottom invertebrates. Thus, in our main series they constitute off Ven 0.51 per cent (*Nauplia* 0.40 and *Cypris* larvae 0.11 per cent), and off Helsingør 0.73 per cent (*Nauplia* 0.56 and *Cypris* larvae 0.17 per cent) of the total stock of bottom animal larvae. Further, the difficulty in determining several of them i. a. owing to their small size and their varying stages in the course of the development of the individual species has forced us to neglect them to the benefit of more significant groups and to number them and note them down as "Cirriped larvae" without referring them to their species and their stage of development.

In modern time papers dealing with the *Cirripedia* from the Sound have been published by Krüger (1927 a, b), Stephensen (1933), Poulsen (1935), Brattström (1936), and Terslin (1940), in which the following adult species are mentioned from the Sound:

Thoracica: Scalpellum scalpellum, (*Lepas anatifera*), (*Lepas hellii*), (*Conchoderma virgatum*), *Verruca stroemia,* (*Balanus tintinnabulum*), (*Balanus nigrescens*), *Balanus improvisus,* (*Balanus amphitrite*), *Balanus balanus = porcatus, Balanus balanoides,* and *Balanus crenatus.*

Ascothoracica: Ulophysema öresundense.

Rhizocephala: Peltogaster paguri, Sacculina carcini, Drepanorchis (*Sacculina*) *neglecta* (taken on a female of *Macropodia rostrata* S. of Lappegrunden, depths 10—15 m, on $^{31}/_{7}$-1941, by the present author), *Lernæodiscus ingolfi,* and *Clistosaccus paguri.*

The *Thoracica* placed between brackets have only accidentally been transported to the Sound by ships and may hardly be reckoned to the fauna. When these species are excluded, we know from the Sound 12 species of *Cirripedia,* viz. *Thoracica* 6, *Ascothoracica* 1, and *Rhizocephala* 5. — The list below briefly gives their occurrence in the Sound and the papers in which their breeding habits and larval development are mentioned.

Scalpellum scalpellum (Linné). Northern part of the Sound at greater depths, not very common. — Breeding habits: Krüger (1920, 1922), Callan (1941). Larvae: Darvin (1851, *Nauplius,* fig.), Lang (1878, *Nauplius,* figs.), Hoek (1909, fig.), Nilsson-Cantell (1921, *Nauplius,* figs.), Krüger (1922), Broch (1924, *Cypris,* p. 19, fig. 4 a—d), and Bassindale (1936, *Nauplius* I, fig.).

Verruca stroemia O. F. Müller. Northern part of the Sound, not very common. — Larvae: Bate (1851, *Nauplia,* figs. with few details only), Hoek (1909, discussion only), Nilsson-Cantell (1921, *Nauplius* I, II, *Cypris*, figs.), Bassindale (1936, description of all 6 *Nauplius* stages and figs. of *Nauplius* I—VI). Metamorphosis: S. Runnström (1927 d).

Balanus improvisus Darwin. Throughout the Sound, common. — Breeding habits: van Breemen (1934), Lucks (1940). Larvae: Münter & Buchholz (1870, *Nauplius* I—II, figs., cfr. also Hoek 1909, figs.), Tengstrand (1931, *Nauplia*, *Cypris*, figs.), Lucks (1940, *Nauplius* IV, VI, *Cypris*, figs.).

Balanus balanoides (Linné). Northern part of the Sound, rather common. — Breeding habits: S. Runnström (1925). Larvae: Bate (1851, figs.), Hoek (1876, figs.), Delsman (1917), S. Runnström (1925, *Nauplius* I, II, *Cypris*, and metamorphosis, figs.), Bassindale (1936, *Nauplius* I, IV, V, description of all 6 stages).

Balanus balanus (Linné) — **B. porcatus** Da Costa. Northern and middle parts of the Sound, rather common. — Larvae: Bate (1851, very rough figs. only). No later descriptions.

Balanus crenatus Brugière. Throughout the Sound, common. — Larvae: Bray (1922, figs.), Herz (1933, good figs. of all 8 *Nauplius* stages, *Cypris* and metamorphosis). Metamorphosis and attachment: Bohart (1929).

Peltogaster paguri Rathke. Northern part of the Sound, not common. New find: 1 spm. was taken on *Eupagurus bernhardus* between Helsingør and Snekkersten, depth 16—18 m, on $^{3}/_{7}$-1941. — Breeding habits: Reinhard (1942 a, b, and c). Larvae: Nilsson-Cantell (1921, p. 100, *Nauplius* I, fig.).

Sacculina carcini Thompson. Northern part of the Sound, not common. — Breeding habits: Delage (1884), Day (1935), Orton (1936 a), and Foxon (1940). Larvae: Delage (1884, *Nauplia* and *Cypris*, cfr. also Hoek 1909).

Drepanorchis (Sacculina) neglecta (Fraisse). One specimen on *Macropodia rostrata* ♀, taken S. of Lappegrunden, depth 10—15 m, on $^{31}/_{7}$-1941. — Larvae: Smith (1906, pl. 4, fig. 17, *Nauplius* I, and fig. 19, *Cypris*).

Lernæodiscus ingolfi Boschma. On *Munida bamffica* on the Gilleleje Flak, depths 32 m, in the northern part of the Sound (cfr. p. 337). — Larvae: Brinkmann (1936, pl. III, fig. 14, *Nauplius* I, fig. 15, *Nauplius* II).

Clistosaccus paguri Lilljeborg. Northern part of the Sound, rare. — Larvae: Boschma (1928, p. 33, *Cypris* in the egg membrane, fig.; the larva emerges in the *Cypris* stage).

Ulophysema öresundense Brattström. Northern and middle parts of the Sound, common. Eggs, embryos and larvae: Brattström (1936, *Nauplius*, *Metanauplius*, *Cypris*, figs.).

Although the Cirriped larvae in our main series have not been identified it can be stated with certainty that no *Nauplia* of the *Lepas* or *Conchoderma* types (as figured i. a. by Groom 1895, Willemoës-Suhm 1877, cfr. also Hoek 1909 and Stephensen 1933) occurred. The *Nauplia* of *Scalpellum scalpellum*, however, may have been confused with the *Nauplia* of *Ba-*

lanus, which totally dominated the Cirriped plankton with the *Nauplia* of *Balanus improvisus* as the most common larvae. The larvae of *Rhizocephala* have never been observed in our samples, but may, examined in broad features as they are, have been overlooked or confused with Balanid larvae. The larvae of the Ascothoracid *Ulophysema öresundense* have, however, specially been sought for several years. They deviate considerably from those of the other suborders and have hardly been overlooked. Their absence from our plankton series seems thus to show, that their pelagic life is very short.

Cirriped larvae, *Nauplia* as well as *Cypris* larvae, occur in the Sound plankton in any month of the year. There are no distinct seasons, but as a rule they are most frequent within the months February-March to July, especially in April to June, and few in number from late in July to November, especially rare in August.

B. Decapoda.

During our investigations the *Decapoda* were less thoroughly studied than most other groups of invertebrates. The reasons for this are: 1) Our standard nets, so suitable for collecting most other planktonic larvae, seem to be too small to secure a sufficiently large number of Decapod larvae to enable us to give a reliable account of their number of species and specimens at the different seasons; and 2) Most of the Danish Decapod larvae have previously been so well described and figured that it seems reasonable to neglect them for the benefit of the more poorly known larval groups.

When the material was worked up for the present paper it turned out that this paper comprised so many larvae of bottom invertebrates that it might serve as a provisional handbook, and from this point of view it was, of course, regrettable that the Decapod larvae had been so superficially treated. I therefore tried to collect all the available information on the reproduction of each single species, i. e. all data on berried females and planktonic larvae not only from the Sound but also from the inner Danish waters in order to give the rough outlines of their breeding habits and larval occurrence.

While our three-year main-series from Ven were treated in very broad features as far as Decapod larvae are concerned (the larvae were often listed merely as "crab-*Zoëa*" or "prawn-*Zoëa*") the larvae of our one-year series taken off Helsingor have been carefully identified and noted down. Further, cand. mag. Th. Kanstrup has very kindly placed a valuable collection of Decapod larvae from the Sound plankton at my disposal. The samples were mainly taken off Snekkersten in the years 1928 to 1938 and had in part been determined and worked up by Mr. Kanstrup when handed over to me. The larvae determined by him have been checked, and the remaining Decapod larvae have been identified by the present author. Finally, the collections of the Copenhagen museum contain several finds of berried females and planktonic larvae from other Danish waters which have helped to fill up the gaps and to enable us to form an estimate of the breeding seasons and larval occurrence in our seas.

The following authors have contributed to our knowledge of the distribution of the Decapod fauna in the Sound: Ørsted (1844), Meinert (1893), Lönnberg (1898, 1899), Stephensen (1910 a, b), Björck (1913, 1915), and Terslin (1940). — During the last few years two further species have been added to the fauna of this area, viz. *Cancer pagurus* (adults as well as larvae) and *Porcellana longicornis* (*Megalopa*). Further, *Pontophilus spinosus*, hitherto only known as a larva, has now been recorded in an adult specimen. Thus, if *Nephrops norvegicus* (larvae taken off Snekkersten) and *Munida bamffica*, both found in large numbers on the Gilleleje Flak off the northern entrance of the Sound, are considered to belong to the fauna of the Sound, we know at present 37 species of *Decapoda* from this area.

Descriptions and figures of the larvae of 35 out of these 37 species are known, the larvae thus being much better known than those of most other groups of bottom invertebrates. As the main papers on Decapod larvae from northern seas I regard those of GURNEY (1903, 1923, 1924a, b, c), LEBOUR (1927, 1928, 1930, 1931a, b, 1937b, 1940a, b, 1943), G. O. SARS (1874, 1884, 1889, 1890, 1899, 1906, 1912), and WILLIAMSON (1900, 1901, 1903, 1904, 1905a, b, 1911, 1915), and valuable investigations have further been published by several other scientists, i. a. APPELLÖF (1909a, b), Miss BERKELEY (1930), BULL (1939), CANO (1893), EHRENBAUM (1907), FAXON (1880), MORTENSEN (1897b), and GLADYS WEBB (1921). The keys in the "Danmarks Fauna" by STEPHENSEN, although published as early as 1910, have been very helpful in the determination of the larvae. Among the many papers on breeding habits, special attention should be paid to those of BOAS (1880, 1889, 1890), BROEKHUYSEN (1937), EHRENBAUM (1890, 1896), HAVINGA (1929, 1930), HJORT & RUUD (1938), JÄGERSTEN (1936), H. & L. NOUVEL (1935, 1937, 1939), and SOLLAUD (1912, 1919, 1921, 1923, 1924). GURNEY has recently (1942) published a monograph on larvae of Decapod Crustacea, and (1939) a "Bibliography of the Larvae of Decapod Crustacea", in which the whole literature on Decapods is gathered.

Most of the Decapod larvae collected in the Sound, thus all the larvae from Snekkersten, are kept in the Copenhagen museum.

Crangon crangon LINNÉ (= **Cr. vulgaris** FABR.). Very common throughout the Sound.

Reproduction: A. Literature. Several authors have contributed to our knowledge of the breeding habits and larval development of this species, i. a. KINGSLEY (1887, 1889), G. O. SARS (1890), EHRENBAUM (1890), WILLIAMSON (1901, 1915), JACKSON (1913a), DONS (1915), GLADYS WEBB (1921), OLGA JORGENSEN (1923), HAVINGA (1930), LEBOUR (1931a), MEYER (1934, 1935), and NOUVEL (1937, 1939). — Their results may be briefly summarised as follows: Adults, which only exceptionally attain an age of three years, are sexually mature when one year old. Mating takes place immediately after the female has moulted, and spawning from a few hours to two to four weeks after mating, but the females may spawn even if no mating takes place. Females about to spawn take in no nourishment and hide in dark sheltered places. During spawning the abdomen is bent forwards and pressed towards the thorax, and the eggs, ejected in chains from the two oviducts, are arranged by the pleopods into large lumps, which at last attach to the pleopods (not to the ventral side of the abdomen), glued together by a hardened slime. Each female breeds two times during the summer (March-April and June) and one time during the winter (September-February), but mating may take place all the year round. Newly spawned summer-eggs (370 μ in longest diameter) are smaller than the corresponding winter-eggs (430 μ). Eggs in the earliest stages of development are whitish and nearly spherical, while those with embryos ready to hatch are greenish, with pigment, much bigger, and shaped like a hens' egg. Small females have 1,500 to 6,000 and large females 9,000 to 14,000 eggs per batch, and as three batches are spawned in a year, the number of eggs produced per female per year may be estimated at about 10,000 to 35,000. The eggs spawned in the winter and exposed to low temperatures will take much longer time to develop (hatching early in spring) than the eggs spawned in the summer (one to two months from spawning to hatching). During the last weeks before hatching the female will take care of the eggs, i. a. aërating and cleaning them by movements of the abdomen. The larvae hatch as *Zoëa*-stages, which immediately ascend to the surface and are highly photopositive. There are five pelagic larval stages, the fifth being converted into a young form like the parents (G. O. Sars 1890, figs., Williamson 1901, figs., 1915, figs., Gurney 1903, key only, Gladys Webb 1921, fig., Lebour 1931a, figs., and key). The larvae occur in the plankton from early spring to autumn, and the pelagic life will take about 5 weeks, i. e. there is about one week between two moultings. Wollebæk (1908, p. 26) mentions berried females off Bergen from August to December (deep water), and Björck (1913) found numerous berried females in the Sound (mostly early eggs) early in July and, decreasing in number, in late July and early August. Early in October females were found with early eggs and eggs nearly ready to hatch. Larvae (especially later stages) occurred in the Sound plankton in July and September.

B. Own remarks. Planktonic larvae were taken in the Sound off Ven on $^{4}/_{8}$-1928 (10 larvae, stage I to IV), $^{17}/_{5}$-1939 (7 larvae) and $^{4}/_{6}$-1939 (2 larvae), off Snekkersten on $^{2}/_{8}$-1928 (2 larvae, stage III—IV), $^{24}/_{9}$-1928 (3 larvae, stage II—IV), $^{26}/_{9}$-1928 (1 larvae, stage V), $^{22}/_{7}$-1930 (3 larvae, stage I), $^{13}/_{9}$-1931 (2 larvae, stage I—II), $^{22}/_{7}$-1932 (41 larvae, all stages), $^{30}/_{7}$-1933 (3 larvae, stage I), $^{2}/_{8}$-1935 (1 larva, stage IV), and $^{21}/_{8}$-1938 (1 larva, stage I), and off Helsingør on $^{17}/_{9}$-1941 (12 larvae) and $^{7}/_{10}$-1941 (2 larvae). Thus the larvae seem to be present from the middle of May to early October, which agrees rather well with the observations of Björck (1913, see above). — The collections of the Copenhagen museum include berried females from Randers Fjord (E. Jutland) collected in May (early eggs), June (late eggs), and August (early and late eggs), and from Frederikshavn in late July (rather early eggs), and larvae from Kattegat plankton taken in early April (very common) and early October (common).

Crangon allmanni Kinahan. Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Dons (1915) mentions females in berry from N. Norway in March and September. Olga Jorgensen (1923), recording pelagic larvae of this species from the Northumberland coast in May to July, adds that there appears to be "a double hatching season, the second one beginning rather later, towards the end of July and continuing until September". This seems to agree well with the two summer-batches known for *Crangon crangon* (which see). At Plymouth (Lebour 1931a) breeding begins in January; the newly spawned eggs measure 800 × 480 μ, and hatching takes place in spring. Early planktonic larvae occur in January to June, later stages in spring and summer. Descriptions of the pelagic larvae, five stages in all, are given by G. O. Sars (1890, figs.), Gurney (1903, key only), Williamson (1915, figs.), Gladys Webb (1921), and Lebour (1931a, figs. and keys). Wollebæk (1908) found berried females off W. Norway in March and throughout spring and summer, and states that the larvae are hatched during the summer months. — Björck (1913, p. 20) found berried females with early eggs in the Sound early in July, with late eggs from late July to early October, and mentions planktonic larvae from the middle of July to early October.

B. Own remarks. Planktonic larvae were taken in the Sound off Snekkersten on $^{29}/_{6}$-1928 (1 larva, stage V) and $^{22}/_{7}$-1930 (5 larvae, stage I—V), and off Helsingør on $^{10}/_{4}$-1942 (7 larvae), $^{22}/_{4}$-1942 (8 larvae, all stages), $^{15}/_{5}$-1942 (2 larvae), $^{4}/_{6}$-1942 (2 larvae), $^{20}/_{6}$-1942 (2 larvae), $^{17}/_{7}$ to $^{18}/_{7}$-1942 (2 larvae), and $^{25}/_{7}$-1942 (6 larvae). Thus the larvae have been seen from the middle of April to late July, i. e. a period very different from the season mentioned by Björck (1913, see above). — In larvae from the Sound the lateral spines on the fifth abdominal segment are less prominent than in the Norwegian specimens sketched by Sars and much smaller than in the British specimens sketched by Lebour. — In the Copenhagen museum there are berried females from the Kattegat taken about the middle of May (early eggs), and from Bohuslän from early May (early eggs).

Pontophilus spinosus LEACH. Taken by the present author north of Ven, depth 40 m, on $^4/_8$-1926.

Reproduction: A. Literature. The breeding habits seem to be unknown. The planktonic larvae are described by G. O. SARS (1890, figs., see also WILLIAMSON 1915, figs.), and a key is given by GURNEY (1903). OLGA JORGENSEN (1923) observed planktonic larvae in stages I, II, and III off the Northumberland coast in May and July. — BJÖRCK (1913) mentions a single larva from the Sound plankton taken in October.

B. Own remarks. No larvae have been observed in our plankton samples from the Sound, the only record being that of BJÖRCK (1913, see above). — Numerous larvae from Kattegat plankton taken on $^6/_4$ to $^{20}/_4$-1935, are found in the Copenhagen museum.

Philoceras bispinosus (HAILSTONE & WESTWOOD) (= **P. nanus** KRØYER). Northern part of the Sound, rather common; middle part of the Sound, scattered specimens.

Reproduction: A. Literature. The breeding habits seem to be unknown. The planktonic larvae have been dealt with by G. O. SARS (1890, figs., see also WILLIAMSON 1915, figs.), GURNEY (1903, keys only), and LEBOUR (1931 a, figs. and keys). At Plymouth eggs ready to hatch measure 480 × 320 μ, the breeding season being in spring and summer, and during these seasons the larvae are fairly common in the plankton (LEBOUR l. c.). — BJÖRCK (1913) found early larvae and post-larvae in the Sound in July and late *Zoëae* and post-larvae in September and early October.

B. Own remarks. Planktonic larvae were taken in the Sound off Snekkersten on $^{21}/_9$-1928 (two early and one late larva), $^{26}/_9$-1928 (6 larvae in late stages), and $^{21}/_8$-1938 (1 late larva), a season agreeing fairly well with the observations of BJÖRCK (1913, see above). — The collections of the Copenhagen museum contain berried females taken in northern Kattegat in late July to the middle of October (eggs in all stages) and in the area round the Skaw in July to November, and larvae from Kattegat plankton taken early in October.

Athanas nitescens (MONT.). Mentioned by MEINERT (1893, p. 224) from the Sound.

Reproduction: A. Literature. The breeding habits have been described by H. & L. NOUVEL (1935, 1937) from Roscoff: Breeding season from late May to the middle of August. When mating, immediately after the female has moulted, the male bends round the ventral side of the female in a line with the first abdominal segment and transversely to the longitudinal axis of the female body. The mating lasts only for a second or so, and the individual male may mate with the same or different females up to four or five times per minute. Spawning takes place a few minutes later; the abdomen is pressed towards the ventral side of the thorax, and the fifth pair of pereiopods arrange the newly spawned eggs into lumps for adhesion to the pleopods. Isolated females will moult at certain intervals, but if not fertilised, will resorb their ripe eggs instead of spawning them. Moulting normally takes place at night, mating immediately afterwards, and spawning in the morning. Sixteen to seventeen days will elapse from spawning to hatching, and a few days after hatching the female, in the breeding season, will be ready to moult, mate, and spawn again. — G. O. SARS (1906) describes and figures the larvae from Oslofjord plankton (redescribed by WILLIAMSON 1915). The eggs are rather large, and the pelagic development somewhat shortened. Sars (l. c.) only followed the development from the plankton larvae — not from the egg, but according to Sars at least five pelagic stages seem to occur. Gladys Webb (1921) describes and figures, from Plymouth, two pelagic larval stages of this species younger than all the stages described by Sars.

B. Own remarks. Planktonic larvae were taken in the Sound off Snekkersten on $^{22}/_{7}$-1930 (2 larvae like fig. 3, and 1 larva like fig. 4 of Sars 1906); $^{30}/_{7}$-1933 (1 larva with a well developed telson, but still without pleopods), and $^{2}/_{8}$-1935 (1 larva like Sars's fig. 1).

Spirontocaris gaimardi (Milne-Edwards). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. The breeding habits seem to be unknown. Lebour (1940 a, with keys to British *Spirontocaris*-larvae) describes and figures the first larvae from Millport. Thorson (1936) has shown that the East-Greenlandic form of *S. gaimardi* has larger and much fewer eggs (probably shortened development) than those from boreal seas, which have a long pelagic life.

B. Own remarks. Planktonic larvae of a species of *Spirontocaris*, the closer identity of which could not be ascertained, were taken in the Sound off Ven on $^{26}/_{8}$-1938 (1 larva), and off Helsingor on $^{7}/_{10}$-1941 (2 larvae) and $^{5}/_{9}$-1942 (1 larva). As *S. gaimardi* is the only common species in the Sound, it seems most reasonable to assume that the larvae belong to this species.

Spirontocaris lilljeborgi (Danielssen). Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. The breeding habits seem to be unknown. Lebour (1937b, figs., 1940 a, keys to larvae of *Spirontocaris* and of related genera) states that the breeding season at Millport, Cullercoates, and Plymouth is December to April (eggs with larvae ready to hatch measure 960 × 1200 μ in diameter), and describes and figures the newly hatched larvae.

B. Own remarks. See the remarks under *Spirontocaris gaimardi.* — In the Copenhagen museum there is a berried female with late eggs from northern Kattegat, taken on $^{22}/_{3}$-1904.

Spirontocaris spinus (Sowerby). Knähaken (1 spm.) and Öretvisten (1 spm.), i. e. both from the middle part of the Sound.

Reproduction: A. Literature. The larvae of *S. spinus* seem to be totally unknown (cf. Lebour 1940 a, p. 505).

B. Own remarks. No observations from the Sound.

Spirontocaris pusiola (Krøyer). Northern and middle parts of the Sound, rare.

Reproduction: A. Literature. The breeding habits seem to be unknown. Dons (1915) mentions that the breeding season off N. Norway is from late April to late August. Bull (1939) found females in berry off Cullercoates throughout the year with a main hatching of larvae between March and August, and describes and figures the first pelagic stages. Lebour (1940 a) gives a key to all the British *Spirontocaris*-larvae. The later larval stages are unknown.

B. Own remarks. No observations from the Sound.

Hippolyte varians Leach. Northern and middle parts of the Sound, rare.

Reproduction: A. Literature. Data on breeding are given by Nordgaard (1912, from W. Norway), and H. & L. Nouvel (1937, from Roscoff): Breeding seasons July to August

(Roscoff) and June to September (Norway). The females, whether fertilised or not, spawn a few hours after moulting, but if not fertilised, the eggs will be cast off within a few days. Twelve to thirteen days elapse from spawning to hatching. Off the British coasts larvae are recorded in the plankton from May to July and August to September (off Northumberland, JORGENSEN 1923), in April (Irish Sea, JACKSON 1913 a), and in summer (off Plymouth, LEBOUR 1931 a). — The eggs are small (400 × 280 μ, young eggs?, LEBOUR 1931 a, to 460 × 340 μ, eggs ready to hatch, SARS 1912), and there are five pelagic stages, described by BATE (1856, fig.), G. O. SARS (1912, figs. of the whole development, see also WILLIAMSON 1915), GLADYS WEBB (1921, fig. of first larval stage), and LEBOUR (1931, figs. of last larva and post-larva). LEBOUR (1940 a) further gives a key to the larvae of *Spirontocaris*, *Hippolyte*, and *Thor*. — BJÖRCK (1913) mentions, from the Sound, a berried female with early eggs from $^{17}/_{7}$-1910, and pelagic larvae in stage V from the middle of July.

B. Own remarks. No larvae have been seen in our plankton samples from the Sound. — In the Copenhagen museum there is a berried female with eggs ready to hatch taken in the Aalbæk Bugt (NW. Kattegat), depth 7 m, on $^{8}/_{10}$-1904.

Pandalus montagui LEACH. Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. JÄGERSTEN (1936) records protandry in this species from Bohuslän: About sixty per cent of the adult animals are protandric hermaphrodites, i. e. in the autumn of the year after their birth (when $1^{1}/_{2}$ years old) they will function as males, but next autumn the same specimens, then $2^{1}/_{2}$ years old, will function as females. Thirty to thirty-five per cent of the adults are "primary females", i. e. they function as females in the autumn of their second year ($1^{1}/_{2}$ years old) exhibiting no male characters and having not previously functioned as males, and a few per cent are "secondary females", i. e. they have purely female gonads and female pleopods, but show traces of reduced male sexual openings and rudiments of vasa deferentia. — LELOUP (1936) studied the sex-conditions in animals from the southern North Sea preserved in formalin. He found the same purely "primary females" as JÄGERSTEN, but is of opinion that the hermaphroditic specimens (externally looking as males) after functioning as males will convert their gonad into an oogonium, which, however, will never reach the stage of spawning. The observations made on *Pandalus borealis* (which see) and those of Miss BERKELEY (1930) on other species of *Pandalus* seem, however, to support the observations of JÄGERSTEN rather than those of LELOUP. The latter author is of opinion that the "primary females" are able to spawn in their second year and again in their third and fourth years. The larvae, which occur in the British plankton in April (Irish Sea, JACKSON 1913 a) and July to August (off Northumberland, JORGENSEN 1923), have been described and figured by G. O. SARS (1900, third and last larval stage resp., fide LEBOUR 1940 b), WILLIAMSON (1915, redescription after SARS), GLADYS WEBB (1921, first larval stage), and LEBOUR (1940 b, with discussion of earlier descriptions). — WOLLEBÆK (1908) mentions berried females from N. Norway in March to early June and a single berried female from W. Norway from late November. — BJÖRCK (1913) found larvae in the Sound from the middle of July to October, the later larvae being dominants during the last part of the season.

B. Own remarks. Planktonic larvae were taken in the Sound off Snekkersten on $^{11}/_{7}$-1929 (2 larvae, stage III—IV), and $^{22}/_{7}$-1930 (16 larvae in all stages, late stages predominant), off Ven on $^{18}/_{8}$-1939 (1 larva), and off Helsingør on $^{15}/_{5}$-1942 (1 larva), and $^{6}/_{7}$-1942 (1 larva), the larval season thus being from the middle of May to October, if the records of BJÖRCK (1913, see above) are also taken into consideration. — In the Copenhagen museum are found berried females from the middle part of the Kattegat taken on $^{12}/_{3}$-1903 (rather early eggs), and from the area round the Skaw taken on $^{7}/_{3}$-1903 (late eggs).

Pandalus borealis Kroyer. Northern and middle parts of the Sound, rather rare.

Reproduction: A. Literature. The breeding habits and sex-conditions have been described and discussed by Wollebæk (1903, 1908), Björck (1911), Dons (1915), Miss Berkeley (1930), Leopoldseder (1934), Stephensen (1935), Jägersten (1936), Hjort & Ruud (1938), Birger Rasmussen (1942, 1945, 1946), and Poulsen (1945). At Bohuslän Jägersten (1936) found that about 90 per cent of all the adults were protandric hermaphrodites, i. e. in the autumn of the year after their birth ($1^1/_2$ years old) they will function as males, but next autumn the same specimens (now $2^1/_2$ years old) will function as females and will continue to do so during the remaining part of their lives, being about four years old before their growth is completed. Off W. Norway some of the "males" $1^1/_2$ years old will function as males also next year when $2^1/_2$ years old, and then they will gradually change their sex, spawning for the first time as females when $3^1/_2$ years old (Birger Rasmussen, 1945, see also Nature, Vol. 157, No. 3981, p. 203, 1946). At Spitsbergen the male and female phases will be reached when the animals are four and six years old respectively. About 5 to 10 per cent are "primary females" (for explanation see *Pandalus montagui*), and only a few per cent are "secondary females". Hjort & Ruud (1938), discussing the results of Jägersten as compared with those of Miss Berkeley (1930) and Leopoldseder (1934), regard all categories of mature individuals mentioned as "the result of a labile equilibrium between male and female potentialities". — The spawning season at Spitsbergen sets in earlier than in more southern waters. Off W. Norway breeding takes place from July to November, off S. Norway from September to November. About 5 months will elapse from spawning to hatching (the larvae hatch in February-March to April-May) off Norway (6 to 8 months off W. Greenland, Stephensen 1935), and soon after the larvae have hatched the mature "females" will prepare a new batch of eggs, the distended bluish ovaries showing through the shell. — The pelagic life takes about 3 months off W. Norway (4 months or more off W. Greenland), and comprises six pelagic stages thoroughly described and figured by Miss Berkeley (1930), while the larvae described by G. O. Sars (1900, cf. also Williamson 1915, p. 365), and Björck (1911) belong to other species, according to Hjort & Ruud (1938) and Lebour (1940b).

B. Own remarks. No observations from the Sound.

Pandalina brevirostris (Rathke). Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. The breeding habits are only little known. Nordgaard (1912, from W. Norway) records females in berry (early eggs) in June to July, Dons (1915, from N. Norway) berried females from March and early April, and Wollebæk (1908, S. Norway) berried females from the middle of March to August, when the larvae hatch. The breeding season thus seems to be in spring and summer, unlike e. g. that of *Pandalus borealis*, which breeds in autumn and winter. — In British plankton the larvae occurred from May, during the whole summer, with post-larvae in September (off Northumberland, Jorgensen 1923), and in April and September (Irish Sea, Jackson 1913a). — There are eight pelagic stages, described and figured by G. O. Sars (1899, 1900, see also Williamson 1915), and Lebour (1940b). The larvae closely resemble those of *Pandalus montagui*, but are of a much smaller size, with a very small rostrum, and have no legs in the first stage. — Wollebæk (1908, p. 69) mentions, from W. Norway, that the species spawns in spring and the larvae hatch in summer. — Björck (1913) mentions, from the Sound, berried females from the middle of July (eggs in all stages) and planktonic larvae from September to early October.

B. Own remarks. Planktonic larvae were taken in the Sound off Ven on $^{4}/_{8}$-1928 (15 larvae, all stages), off Snekkersten on $^{2}/_{8}$-1928 (1 larva in stage I, 1 in last stage), $^{2}/_{9}$-1928 (45 larvae, all stages), $^{21}/_{9}$-1928 (11 larvae, all stages), $^{21}/_{10}$-1928 (1 larva in stage II, 3 larvae in last stage), $^{9}/_{8}$-1929 (1 early larva), $^{22}/_{7}$-1932 (19 larvae, all stages), and $^{21}/_{8}$-1938 (4 larvae in the two last stages), and off Helsingør on $^{17}/_{9}$-1941 (1 larva), $^{17}/_{7}$-1942 (1 larva), and $^{5}/_{9}$-1942 (1 larva). The larval season is thus from the middle of July to late in September, which is is good agreement with the data given by Björck (1913, see above). — Berried females from the northern part of the Sound taken on $^{1}/_{8}$-1941 (early eggs), and from the Kattegat from late June to late August (all females with early eggs), are found in the Copenhagen museum.

Leander (Palæmon) adspersus var. **fabricii** Rathke. Common throughout the Sound.

Reproduction: A. Literature. Winther (1874, pp. 319—20, as *Palæmon squilla*) mentions late June and July as the breeding season in the Sound. Mortensen (1897 b, cf. also Williamson 1915) gives a detailed account of the biology of this species in Danish waters, especially the Limfjord: Males as well as females reach sexual maturity when one year old. The whole life of a male seems to be two years, that of a female three years. Breeding season from early May to July. Already in April the ovary with its mature, dark-green ova is visible through the shell, and the eggs are spawned immediately after the female has moulted. The mating was not observed, and the size of the eggs is not given. During spawning the abdomen is bent towards the ventral side of the thorax, and the eggs adhere to the pleopods embedded in a hardened slime. The large females will spawn earlier in the season than the younger ones, and a female carries from 300 to 2,500 eggs on its pleopods, according to its size. About one month will elapse from spawning to the hatching of the larvae; several females will moult immediately after the larvae have hatched, and will spawn again the next day. Thus, two batches per female per summer is a normal feature in the larger females. — Planktonic larvae occur in the Limfjord from early June to late August (September). The larvae swim backwards with the dorsal side downwards and have their main occurrence in the open sea. Mortensen (l. c., see also Williamson 1915, pp. 393—96) describes and figures the five pelagic stages, which, according to Gurney (1924 a), seems to be the normal number of larval stages within northern *Palæmonidae*. The pelagic life takes four (from three to five) weeks, and after the fifth moulting the pelagic larva, now 7 to 8 mm long and shaped very much like the adults, seek to the bottom and migrates to shallow water. — Björck (1913) mentions berried females from the Sound in July.

B. Own remarks. Planktonic larvae of *Leander sp.*, presumably belonging to this species, were taken in the Sound off Helsingør on $^{4}/_{6}$-1942 (1 larva), and $^{18}/_{7}$-1942 (2 larvae). — The collections of the Copenhagen museum include a berried female from Frederikshavn (NW. Kattegat) taken on $^{27}/_{6}$-1904 (early eggs), and a few larvae from Kattegat plankton taken in early April and early October.

Leander (Palæmon) squilla (Linné). Common throughout the Sound.

Reproduction: A. Literature. Mortensen (1897 b, p. 27) suggests that two spawnings per season take place in Danish waters. Nordgaard (1912) found females in berry off W. Norway in June. — Gurney (1923) and H. & L. Nouvel (1937) describe the breeding habits from

Norfolk and Roscoff resp.: Breeding season from late May or early June to the middle of August or early September, i. e. about 100 days. Animals one year old are sexually ripe, but females two years old spawn earlier in the season than the younger females. Moulting takes normally place at night, and mating a few hours later. When mating, the male is bending round the ventral side of the female transversely to the longitudinal axis of the female body. The mating takes some seconds, and only one mating takes place per female per spawning. Spawning takes place a few hours after moulting, also without mating, but unfertilised eggs are cast off in less than 24 hours after spawning. By far the majority of the females produce two batches of eggs per season; the eggs are greenish-grey (NORDGAARD, l. c.); the egg size seems to be unknown. — Five to six weeks elapse from the spawning to the hatching of the larvae, the period varying considerably with the temperature (e. g. at Millport 30 days at 23° C, 40 days at $14^{1}/_{2}$° C, and 56 days at 11° C, cf. ELMHIRST 1921). The pelagic life, comprising five larval stages, is normally spent out at sea and is estimated at about four weeks. Post-larvae occur in Norfolk plankton from the middle of August. STUXBERG (1874) and GLADYS WEBB (1921) give brief descriptions without figures of the larvae, which have been thoroughly dealt with by GURNEY (1924 a), who figures stages I, II, and the first post-larva (as stage V, GURNEY's own correction). — BJÖRCK (1913) mentions, from the Sound, females with young eggs or with hatching larvae from early July.

B. Own remarks. A larva presumably belonging to this species (late stage) was taken in plankton off Snekkersten on $^{2}/_{9}$-1928. — The collections of the Copenhagen museum include a berried female with late eggs taken off Frederikshavn (NW. Kattegat) in July 1909.

Palæmonetes varians LEACH. In brackish water in the middle and southern parts of the Sound, rather common.

Reproduction: A. Literature. MAYER (1881), BOAS (1880, 1889, 1890), MORTENSEN (1897 b), SOLLAUD (1912, 1919, 1921, 1923, 1924), and GURNEY (1923, 1924 b) describe and discuss the breeding habits and development of this species. — There are two biologically different varieties, viz. 1) A brackish-water form, *P. varians microgenitor* BOAS, living along the coasts of N. and W. Europe; the females carry 100—450 eggs, which are 700—800 μ long (Denmark, MORTENSEN, BOAS) to 900—1200 μ long (England, GURNEY 1924 b), and the larvae hatch as 4 mm long *Zoëas* of the normal pelagic type; and 2) A fresh-water form, *P. varians macrogenitor* BOAS, living in lakes and rivers in S. Europe; the females have 20—50 eggs, which are 1300—1400 μ (SOLLAUD) to 1500—1750 μ long (BOAS), and the larvae hatch as clumsy *Zoëas* 5.5 mm long in a much more advanced stage of organisation. A "third variety", "*P. varians mesogenitor* SOLLAUD", living in lakes in Tunisia, which has females with 60—100 eggs (1100—1200 μ long), and larvae which hatch in a stage very like the adults (SOLLAUD 1912) according to GURNEY (1923) seems to be structurally different from the other forms and should be regarded as a distinct species.

The W. and N. European brackish-water form, *P. varians microgenitor*, breeds near England (Norfolk, Plymouth) from April to late in July. Normally only one breeding occurs per female per season, but two breedings may occur (GURNEY 1923). In Danish waters the species seems normally to have two breedings per female per season (MORTENSEN 1897 b, p. 27). In aquaria (England) 5 to 6 weeks elapsed from spawning to hatching, but the development probably proceeds more quickly in nature (GURNEY 1923). Near England "the middle of June may be regarded the main hatching-season". The pelagic larval life may vary from at least 15 to 33 days and from 5 to 8 moultings according to variations in salinity and temperature

(Sollaud 1919). The food conditions seem likewise to influence the duration of the larval life (Gurney 1924b, p. 299). The young pelagic larvae are strongly photopositive, while the just metamorphosed bottom-stages are photonegative (Sollaud 1921).

Sollaud (1923), and Gurney (1924b) give fine descriptions of the pelagic larvae of the NW. European brackish-water-form, which was formerly roughly sketched by Boas (1880, 1890). Very interesting is Gurney's (1924b, p. 299) observation that the larvae off England, though derived from larger eggs, pass through a pelagic development, agreeing in all essentials with that of the larvae derived e. g. from the smaller Danish eggs. There are normally 6 (occasionally 7 or more) pelagic stages (5 moults) before the first post-larval stage is reached. "...from stage 3 onwards the changes between moults become so inconsiderable that there cannot be said to be any true metamorphosis" (Gurney 1924b).

B. Own remarks. No observations from the Sound. — In the Copenhagen museum are found berried females of *P. v. microgenitor* from Amager taken on $^{21}/_{6}$-1944 (3 ♀♀ with late eggs), and from Nykobing Mors (the Limfjord) taken on $^{18}/_{7}$-1906 (3 ♀♀ with late eggs).

Portunus depurator (Linné). Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. The breeding habits are little known. Females in berry are recorded from the Sound in July (Björck 1913) and from Plymouth "in spring, summer and autumn, rarely in winter, chiefly in spring" (Lebour 1928). The light brown to dark brown eggs measure 320 and 400 μ, early and late eggs respectively (Lebour 1928). The planktonic stages are i. a. described by Williamson (1911, fig. of first *Zoëa*, 1915), Björck (1913, first, third, fourth, fifth *Zoëa*, *Megalopa*, and first post-larva with figs., from the Sound), and Lebour (1928, first *Zoëa* and *Megalopa*, with figs., from Plymouth). Planktonic larvae are known from the Sound, occurring mainly in September to October (Björck 1913), and from the Irish Sea in April (Jackson 1913).

B. Own remarks. Planktonic larvae were taken in our plankton samples from the Sound off Snekkersten on $^{2}/_{9}$-1928 (2 larvae in *Pre-Zoëa* stage and 2 larvae in the two last stages), $^{13}/_{9}$-1931 (1 larva, stage IV), $^{2}/_{8}$-1935 (1 larva, stage II), and $^{21}/_{8}$-1938 (2 larvae in stage III, and 2 larvae in stage IV). These data seem to be in good agreement with the observations of Björck (1913, see above). — In the Copenhagen museum we find berried females from the northern part of the Sound (Hellebæk) taken in July 1912 (with early and rather early eggs resp.), and from Frederikshavn (NW. Kattegat) taken on $^{1}/_{8}$ to $^{16}/_{8}$-1935 (rather early eggs), and larvae from Kattegat plankton from early October (very common, all stages).

Portunus pusillus Leach. Two old finds from the northernmost part of the Sound. — Adult specimens were found by the present author at Domsten's reef, depth 12—20 m, algae, on $^{8}/_{7}$-1941, and off Hellebæk, depth 35 m, on $^{12}/_{9}$-1941.

Reproduction: A. Literature. Lebour (1928) gives, from Plymouth, a few data on the breeding and describes and figures the first *Zoëa* (previously figured by Cano 1893, see also Williamson 1915) and the *Megalopa*; she found females in berry from February to August, chiefly in spring and early summer. The orange-red eggs measure 280 and 320 μ across in early and late stages resp. The larvae hatch as *Pre-Zoëa*, soon developing into the first of the five *Zoëa*-stages, and larvae occur in the British plankton in spring and summer.

B. Own remarks. A female taken off Hellebæk on $^{12}/_{9}$-1941 had eggs on its pleopods. No larvae have been observed in our plankton samples from the Sound. — A berried female (early eggs) taken off Frederikshavn (NW. Jutland) in June to July 1909 is found in the Copenhagen museum.

Portunus arcuatus Leach. Old finds from Hornbæk and Hellebæk (Meinert 1893, p. 212). One adult specimen was found by the present author in the northern part of the Sound in the summer of 1941. Unfortunately the specimen was lost, but I distinctly remember the animal, which was typical and easy to identify.

Reproduction: A. Literature. Lebour (1928, pp. 510—11) gives, from Plymouth, a few data on the breeding and describes and figures the first *Zoëa* and the *Megalopa*. Berried females were found from April to September, chiefly in spring. The eggs are reddish, changing to almost black, and measure 260 and 300 μ across in early and late stages resp. The larvae hatch as *Pre-Zoëa*, then follow five *Zoëa*-stages and a *Megalopa*, all common in Plymouth plankton in spring and summer.

B. Own remarks. No observations are known from the Sound. — The collections of the Copenhagen museum comprise some berried females from Frederikshavn (NW. Jutland) taken in June-July 1909 (rather early eggs) and near the Skaw on $^6/_7$-1911 (rather early eggs).

Carcinus maenas Pennant. Extremely common throughout the Sound.

Reproduction: A. Literature. Data on sexual maturity and breeding habits have been given by Williamson (1903, 1904), Orton (1913, 1936b, 1937), Dons (1932, 1933a), Björck (1913), Nordgaard (1912), and Lebour (1928). The fine paper of Broekhuysen (1937) comprises a thorough study of the whole reproduction of this species near Holland. The data given by the authors just mentioned may be summarised as follows: The males may reach maturity at a carapace width of 2.5 to 3.0 cm, the females at 1.9 to 2.0 cm, i. e. for both sexes when less than one year old (Orton 1913, 1936, 1937, Broekhuysen). The breeding season is long: In northern Norway mating was observed from early August to medio November, and females in berry nearly throughout the year (Dons 1933a); in W. Norway mating was observed late in August, and berried females nearly throughout the year (Nordgaard 1912, Dons 1932); at Plymouth the species "is in berry all the year round, although it chiefly breeds in spring and summer" (Lebour 1928, p. 517); off Holland berried females occur all the year round, being however, rare from August to October and commonest in November to December (main spawning) and in spring and early summer (Broekhuysen). The adult males, which seem to be able to copulate throughout the year, will often seek to the females a few days before the moulting of the latter, and the copulation will take place soon after the female has moulted. The newly moulted female will remain passive towards the mature male (Williamson 1904, Dons 1932, Broekhuysen), which turns the female upside down. The female now rises its abdomen, bringing it outside the abdomen of the male, which, having extended its abdomen and rested its telson on the thorax of the female, quickly inserts its penes into the two apertures, pushing the penes into the vaginæ and drawing them slightly out about once every two seconds. The male carries the female about with it, and the female is attached to the male simply by the hooked penes (Williamson 1904, Broekhuysen). The spermatophores from a single mating placed in the copulatory pouches of the female seem to suffice for at least two batches of eggs, and the vitality of the spermatozoa seems to amount to ten months. From $1^1/_2$ to $4^1/_2$ months may elapse from mating to spawning (Broekhuysen). Near Holland 50 to 60 per cent of the females spawn in the autumn a few months after moulting; these eggs hatch in May. The females which produce no eggs in the autumn (about 40 per cent) will probably spawn next spring, while females spawning later in the summer probably comprise those which had eggs already in the preceding winter (Broekhuysen). — The eggs attaching to the pleopods of a large female may amount to 185,000; they are nearly spherical (perhaps somewhat oval), yellowish-brown changing to almost black, measuring 320 μ and 400 μ in diameter in early and late eggs resp. A newly spawned egg mass is light orange-coloured, changing during the development to a deep amber and, in the latest stages, a grey colour (Williamson 1903). In the winter and early spring the eggs use about 5 to 6 months from spawning to hatching.

Larvae have been observed in plankton off Plymouth "especially in spring and early summer" (Lebour 1928), off Scotland from March to late in July (Williamson 1903), off Northumberland from May to August (Jorgensen 1918, 1923), off W. Norway in the summer with *Megalopa* in August (Nordgaard 1912, Dons 1932), and in the Sound from July to October (Björck 1913), having their main occurrence in the summer half-year. They hatch as *Pre-Zoëas*, which several hours later develop into the first *Zoëa* stage. — The larvae are described and figured i. a. by Couch (1843, *Zoëa*, *Megalopa*), Faxon (1880, *Pre-Zoëa* and *Zoëa*), Williamson (1900, 1903, 1915, good figs. of most stages), and Lebour (1928, all four *Zoëa*-stages and *Megalopa*). The *Zoëas* differ from other crab-*Zoëas* by having no lateral spines on the carapace.

B. **Own remarks.** Mating specimens, the female with a soft carapace, were found near Ven on $^{25}/_{7}$-1940. Planktonic larvae were taken in the Sound off Ven on $^{4}/_{8}$-1928 (1 *Pre-Zoëa*, 2 in second *Zoëa*); $^{17}/_{7}$-1928 (2 larvae), $^{1}/_{8}$-1938 (1 larva), $^{13}/_{8}$-1938 (3 larvae), off Snekkersten on $^{2}/_{8}$-1928 (1 larva in second, 6 in third, and 4 in fourth *Zoëa* or later stages), $^{2}/_{9}$-1928 (1 larva in second *Zoëa*, 1 *Megalopa*), $^{30}/_{7}$-1933 (5 larvae in first, 2 in second *Zoëa*), and $^{21}/_{8}$-1938 (1 larva in second, 1 in fourth *Zoëa*), and off Helsingør on $^{17}/_{9}$-1941 (3 larvae), $^{18}/_{7}$-1942 (1 larva), $^{25}/_{7}$-1942 (11 larvae), and $^{17}/_{8}$-1942 (1 larva), the season thus being from the middle of July to the middle of September. — The Copenhagen museum contains a few larvae from Kattegat plankton from early October 1935 and several *Megalopa* and first post-larval stages from Frederikshavn (NW. Kattegat) from August 1903. — Analyses have been made on a large number of *Carcinus* from Ven in the Sound, from Ringkøbing Fjord (W. Jutland, brackish water), and from Nykøbing Mors and Nissum Bredning (both localities in the Limfjord) in order to ascertain the number of berried females, the proportion between females and males, and the percentage of crabs infected by *Sacculina carcini*.

Locality	Off Ven, depth 0 to 3 m. $^{24}/_{7}$ to $^{7}/_{8}$-1940	Ringkøbing Fjord, depth 0 to 5 m, in the fishermen's nets, $^{18}/_{7}$-1940	Nykøbing, Mors, depth 0 to 8 m, $^{1-18}/_{7}$-1940	Nissum Bredning, depth 0 to 8 m, $^{15}/_{7}$-1940
♀♀ with eggs	0— 0 %	4— 2 %	4— 6 %	1— $3^{1}/_{2}$ %
♀♀ without eggs	17—23 %	71—33 %	15—24 %	13—45 %
♀♀ with *Sacculina*	0— 0 %	0— 0 %	26—42 %	5—17 %
♂♂ without *Sacculina*	57—77 %	143—65 %	9—14 %	9—31 %
♂♂ with *Sacculina*	0— 0 %	0— 0 %	9—14 %	1— $3^{1}/_{2}$ %
Total...	74	218	63	29

It will be seen from the table that *Sacculina carcini* seems to be totally absent in the populations from shallow water off Ven and from Ringkobing Fjord, i. e. the two localities with a low salinity, while the percentage of infected crabs in the Limfjord (high salinity at the surface) is very high, thus off Nykøbing Mors 56 per cent of the whole population. The infection in the Limfjord is so heavy that the crabs have commenced to decrease considerably in number.

Interesting is the fact that off Ven, where the crabs were collected in quite shallow water, and in the Ringkobing Fjord, where the crabs examined were derived from the fishermen's nets, the percentage of males (77 and 65.6 per cent resp.) far exceeds that of the females (23 and 34.4 per cent resp.), and among the females captured the percentage of berried crabs (0 and 1.8 per cent. resp) is extremely low. As the analyses have taken place during the actual breeding season, the figures seem to show that the berried females will hide in somewhat deeper water, remaining there without roaming about. They will not appear in the tidal zone and will not enter the fishermen's nets until the larvae are hatched. Quite similar observations were made in the Gamborg Fjord (near the Little Belt) in July 1914, where male crabs were abundant near the shore, while females were extremely rare. The few females secured in this locality by dredge-hauls at somewhat greater depths all proved to be berried.

Cancer pagurus LEACH. Formerly common southward to Copenhagen (STEPHENSEN 1909, p. 264). — The fisherman MANFRED NIELSEN of Helsingør described to me in all details a specimen taken off Hellebæk, depth 16 m, in December 1941, and other fishermen also reported the occurrence of this species in the Sound, though it was found in scattered specimens and was rather rare.

Reproduction: A. Literature. The breeding habits have been discussed and described by MEEK (1899a), WILLIAMSON (1900, 1904, 1905a), PEARSON (1908), NORDGAARD (1912), and ORTON (1936b). The species seems to be sexually mature when about three years old (ORTON), the whole life of *Cancer pagurus* amounting to nine years at most (PEARSON). The males reach the stage of maturity somewhat earlier than the females. Females may be mature with a carapace width of 12.5 cm, a large proportion of the crabs being mature with a carapace width of 13 to 15 cm, while all crabs with a carapace width of over 13.65 cm were found to be fertilised (WILLIAMSON 1900). Mating takes place in the autumn when the female has moulted. The moulted female is attracted by and moves towards a ripe male, but like *Carcinus* will behave quite passively when discovered and attacked by the male. WILLIAMSON (1904) observed a male which "gathered the female up with its legs and tucked her underneath him". One mating seems to be sufficient for the production of two (in older crabs even three) batches of eggs (PEARSON). A female very often carries eggs two years in succession while moulting only seems to take place every two years. A female which has spawned in two successive years will normally moult and then spawn again 14 months later (the spermatozoa thus being able to survive for at least this period), but it may spawn again already 4 to 5 months after moulting. "We thus have a reproductive period of at least two successive years, followed by an interval of growth to be succeeded by another reproduction period—annual spawning; biennial or triennial growth" (WILLIAMSON 1900).

Spawning takes place off W. Norway in October-December (NORDGAARD) and off Scotland in November-January (WILLIAMSON 1900). Experience from both Norway and Scotland shows that females will spawn in deeper water and then migrate to shallower (warmer) water the more the embryos approach the stage of hatching (NORDGAARD, WILLIAMSON 1900). The number of eggs per batch may vary from 460,000 to 3,000,000 according to the size of the female (MEEK, WILLIAMSON 1900). When newly spawned the whole egg mass is of a beautiful orange colour, changing through more or less reddish to greyish-yellowish colours when the embryos approach the stage of hatching (NORDGAARD, WILLIAMSON 1900). The egg, of a brilliant orange changing to a brownish colour, measures 320 μ and 400 μ in early and late stages resp.

During the last months of the incubation the female will nurse and aërate the eggs, i. a. by movements of its tail. The larvae take about 7 to 8 months to pass from spawning to hatching, the latter process taking place in July and August (MEEK, NORDGAARD, WILLIAMSON 1900) with laggards in September to October (WILLIAMSON 1905 a). — The newly hatched larvae, which are strongly photopositive (NORDGAARD, WILLIAMSON 1905 a), have been described and figured i. a. by WILLIAMSON (1900, 1903, 1911, 1915, *Pre-Zoëa*, first *Zoëa*), PEARSON (1908, *Pre-Zoëa*, first *Zoëa*), NORDGAARD (1912, *Zoëa*), and LEBOUR (1928, first to fifth *Zoëa*, *Megalopa*). The pelagic larval life is estimated at about two months (PEARSON 1908).

B. Own remarks. Planktonic larvae were taken in the Sound off Ven on $^{5}/_{8}$-1939 (1 larva), off Snekkersten on $^{11}/_{7}$-1929 (1 larvae), and off Helsingør on $^{17}/_{9}$-1941 (3 late larvae), $^{15}/_{5}$-1942 (3 larvae), $^{4}/_{6}$-1942 (3 larvae), and $^{5}/_{9}$-1942 (2 early larvae), the season thus extending from the middle of May to the middle of September. — The collections of the Copenhagen museum include larvae from Kattegat plankton taken early in April (a few specimens only) and early in October (common).

Macropodia (Stenorhynchus) rostratus (LINNÉ). Previously known from Hellebæk. — One adult, just moulted specimen was found between Sofiero and Lappegrunden, depth 35 m, on $^{8}/_{7}$-1941; a female with *Drepanorchis neglecta* (cf. p. 319) was taken S. of the Lappegrund light-ship, depth 10—15 m, sand with shells, on $^{31}/_{7}$-1941. Thus the species seems only to occur in the northernmost part of the Sound.

Reproduction: A. Literature. The breeding habits seem to be poorly known. Females in berry at Plymouth all the year round; larvae in plankton nearly all the year round with maxima in spring and summer (Plymouth Mar. Fauna 1931, LEBOUR 1928). The pelagic larvae have been described and figured by CANO (1893, first *Zoëa*, *Megalopa*), and LEBOUR (1927, a few remarks only, 1928, first and second *Zoëa*, *Megalopa*). The eggs are orange-red and measure 450 μ and 580 μ in diameter in early and late stages resp. The larvae hatch as *Pre-Zoëa*. There are two *Zoëa*-stages and *Megalopa*.

B. Own remarks. No observations on larvae or berried females are available from the Sound. — Berried females taken E. of Als (southern part of the Little Belt) on $^{30}/_{6}$-1911 (2 females with early eggs and 6 females with rather early eggs), and 2 larvae from plankton W. of Sejrø on $^{3}/_{10}$-1935, are found in the Copenhagen museum.

Inachus dorsettensis (PENNANT). Known from Gilleleje, Hellebæk, and NW. of Ven, rare.

Reproduction: A. Literature. The breeding habits seem to be poorly known. Near Plymouth the species is in berry throughout the year. "The eggs are reddish-orange when first extruded and remain hidden in the pouch until they are nearly ready to hatch, when the colour changes to a dull pale yellowish-brown and the pouch opens slightly as the eggs occupy more space." Early eggs measure 480 μ, late eggs 720 μ in diameter. "The eggs certainly take some weeks to hatch, probably some months...". "...When one batch of eggs has been hatched another frequently takes its place..." (LEBOUR 1927, 1928). The pelagic larvae, which at Plymouth are to be found in the plankton in any month, are described and figured by CLAUS (1876, first *Zoëa*), CANO (1893, first *Zoëa*), and LEBOUR (1927, *Pre-Zoëa*, first *Zoëa*, second *Zoëa*, *Megalopa*, 1928, first *Zoëa*, first young crab). The planktonic life seems to take about 3 weeks (LEBOUR 1928, p. 547).

B. Own remarks. No observations on larvae or berried females are at hand from the Sound. — In the Copenhagen museum there are two berried females with early and rather early eggs resp. taken on the Lille Middelgrund (E. Kattegat), depth 30 m, on $^{12}/_{7}$-1932.

Hyas araneus (Linné). Northern and middle parts of the Sound, not very common.

Reproduction: A. Literature. Off N. Norway sexual maturity is attained in about three years; the main breeding season is in winter, but females with newly spawned eggs may be met with about the middle of March and late in June. Berried females seem to be able to spawn again the following year (Dons 1912—13, 1915). Off Scotland females in berry are recorded from May and June, the egg mass being of a bright orange colour (Williamson 1911). Berried females will now and then place themselves in a vertical position, nursing their eggs with the chelipeds and aërating them by violent strokes of the tail (Broekhuysen 1937). — The planktonic larvae are recorded from N. Norway in April-May (Dons 1915), from the Irish Sea in April (Jackson 1913a, *Pre-Zoëa*, first and second *Zoëa*), and from Northumberland in May (Jorgensen 1923). They are described by Williamson (1911, first and second *Zoëa*, *Megalopa*, and first young crab, 1915). — The larva from the Sound described and figured by Björck (1913, p. 22) belongs to *Hyas coarctatus*.

B. Own remarks. No observations on larvae in plankton from the Sound.

Hyas coarctatus Leach. Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. Dons (1915) is of opinion that specimens from N. Norway may attain maturity when two years old and mentions several berried females from April to September. Off W. Norway Nordgaard (1912) found females with newly spawned eggs in July and August and with late-stage eggs in March; thus about eight months seem to elapse from spawning to hatching. Lebour (1928), at Plymouth, found berried females in March to December, and "larvae in plankton chiefly in early spring". Off W. Greenland larvae occur in May to August (Stephensen 1913), and in the Sound *Megalopa*-stages were taken in July (Björck 1913). — The eggs are a bright orange changing to an orange-brown, and measure 400 μ and 560 μ in early and late stages resp. (Lebour 1928). — The planktonic larvae are described and figured by Stephensen (1913, p. 128, fig. 33, as "Brachyurid-larva", first *Zoëa*), Björck (1913, p. 22, *Megalopa*), Williamson (1915, several stages from Greenlandic waters), and Lebour (1928, first and second *Zoëa*, *Megalopa*).

B. Own remarks. A berried female with early orange eggs was taken off Hellebæk, depth 30 m, on $^{14}/_{7}$-1941. No larvae have been obtained from our plankton-samples in the Sound. — In the Copenhagen museum there are berried females from the Hanstholm area (the Skagerrak) taken on $^{20}/_{6}$-1911 (early and late eggs), and $^{27}/_{9}$-1913 (early eggs).

Eurynome aspera Leach. One find off Hellebæk several years ago. Not found later.

Reproduction: A. Literature. The breeding habits are only poorly known. At Plymouth (Lebour 1928) berried females occur in spring and summer. The eggs are a bright red, clear and of a darkish shade, and measure 360 μ and 370 μ in early and late stages resp. — The pelagic larvae, common at Plymouth in spring and summer but very rarely in autumn, have been described and figured by Kinahan (1857, *Pre-Zoëa*), Cano (1893, first *Zoëa*), Gurney (1924c, description of *Pre-Zoëa* and first *Zoëa*), and Lebour (1928, first and second *Zoëa*, *Megalopa*).

B. Own remarks. No berried specimens nor planktonic larvae are known from the Sound. — In the Copenhagen museum we find berried females taken off Frederikshavn from late June to early August (eggs in all stages), off the Læsø Trindel in early August (late eggs), off the Store Middelgrund on $^{12}/_{7}$-1932 (rather early eggs), and at Groves Flak on $^{2}/_{8}$-1930 (rather early and late eggs resp.). The breeding thus seems to take place in the actual summer time.

Nephrops norvegicus LINNÉ. Northern and middle parts of the Sound, rare. In the area round Gilleleje Flak off the northern entrance to the Sound, depth 32 m, this species has been the object of a rather considerable fishery in the years 1936 to 1938.

Reproduction: A. Literature. Data on breeding habits are given by NORDGAARD (1912), HAVINGA (1929), HÖGLUND (1942), and POULSEN (1945). The smallest mature animals, about 10 cm long, seem to be about seven years old. Spawning takes place some time after mating, the spawning females lying on their back, and a single batch comprises from 1000 to 5000 eggs. Females in berry may be met with nearly throughout the year, but in Danish waters spawning seems mainly to take place in late spring or in summer (POULSEN). The female seems only to produce one batch every two years. The eggs are greenish to dark green and measure 1370 × 1050 μ and 1120 × 1070 μ (Scotland, WILLIAMSON 1915) or 1400 μ (NORDGAARD 1912, stage of development unknown). About 8 to 9 months elapse from spawning to hatching, the latter process being accordingly at its height in early spring (POULSEN). Off Northumberland, however, "the hatching period is to be reckoned as being of not less than three months' duration" (JORGENSEN 1925). — Larvae in plankton have been recorded from Danish waters in April, July, and October (POULSEN), off Northumberland in May to July (JORGENSEN 1923), and in the Irish Sea in April, May, and August (JACKSON 1913a, JORGENSEN 1923). The larval season thus seems to be long. — The pelagic larvae, easily recognisable by their long dorsal spines on the abdomen and their large characteristic telson, have been described by G. O. SARS (1884, 3 stages, good figs., 1889, last larval stage, fig.; cf. also WILLIAMSON 1915) and SANTUCCI 1926, 1927. — Second- and third-stage larvae seem to be photonegative (JORGENSEN 1925).

B. Own remarks. A single planktonic larva (earliest stage) was taken off Snekkersten on $^{9}/_{8}$-1929, depth 20—0 m. — In the collections of the Copenhagen museum there are a few larvae from Kattegat plankton taken on $^{5}/_{4}$ to $^{7}/_{4}$-1935 and $^{4}/_{10}$-1935, and a very young bottom-stage from Læsø Rende taken on $^{30}/_{7}$-1937.

Homarus vulgaris MILNE-EDWARDS. Recorded by MEINERT (1893, p. 212) from Hellebæk. Not found later.

Reproduction: A. Literature. The breeding habits have been described and discussed i. a. by G. O. SARS (1874), EHRENBAUM (1896, 1907), MEEK (1899b, 1900), SCOTT (1903), WILLIAMSON (1905b), and APPELLÖF (1909a, b). The females off W. Norway attain maturity when 9 to 14 years old, off S. Norway one or two years earlier. The smallest length for mature females off W. Norway is 24—25 cm, off S. Norway 22—23.5 cm, and in more southerly waters 21—22 cm (APPELLÖF). Mating not observed, but sperm placed on the ventral side of the female has a long vitality, females being able to spawn fertilised eggs after a long period of isolation (APPELLÖF). Spawning takes place in July to October with a pronounced maximum from the middle of July to the middle of August (W. Norway, Scotland, Heligoland, cf. APPELLÖF), and in August (near Plymouth, ALLEN 1895—96). — Ten females from W. Norway had on an average 12,600 eggs on their pleopods (APPELLÖF), while nine females from Heligoland had on an average 14,800 eggs, the number of eggs increasing with the size of the females (EHRENBAUM 1896). The newly spawned eggs are dark green and measure 1800 μ in diameter (SCOTT 1903). The berried female nurses and aërates the eggs, at intervals stretching its tail to its full length and moving the pleopods (WILLIAMSON 1905b, APPELLÖF 1909a—b). — The time from spawning to hatching is 11 to 12 months (W. Norway, APPELLÖF), $10^{1}/_{2}$ to $11^{1}/_{2}$ months (S. and E. Norway, APPELLÖF), 11 months (Heligoland, EHRENBAUM 1896) and 9 to

$9^1/_2$ months (Plymouth, ALLEN 1895—96), and accordingly the hatching takes place off W. Norway from July to October with a maximum from the middle of July to the middle of August, and somewhat earlier off S. Norway (APPELLÖF), off Heligoland from the middle of July to the middle of September (EHRENBAUM 1896), off the Isle of Man from July to August (CHADWICK 1905), and off Plymouth from the middle of May to July (ALLEN). The process of hatching a whole batch from a single female takes from one to three weeks (WILLIAMSON 1905b); hatching normally takes place at night. The larvae hatch as first *Zoëa*, they are positively phototactic, and begin to swim immediately after hatching and to chase larvae of *Eupagurus*, *Cancer*, prawns, and copepods; also cannibalism may occur. Off Scotland the pelagic life in July-August at 12.5° C lasts for "a period of, roughly, three weeks" (WILLIAMSON 1905b).

The pelagic larvae, which have a somewhat shortened development, have been described i. a. by G. O. SARS (1874, all stages, good figs.), WILLIAMSON (1905b, figs., 1915, figs.), CHADWICK (1905, figs.), EHRENBAUM (1907, figs.), and APPELLÖF (1909a, b, figs.). There are three pelagic stages only, stage III being a "swimming-crawling stage".

B. Own remarks. No observations from the Sound. — Larvae from Frederikshavn plankton (N.W. Kattegat) taken on $^{23}/_7$-1893 and $^{21}/_7$-1909, are found in the Copenhagen museum.

Lithodes maja LINNÉ. Old records from Hellebæk and Ven (MEINERT 1893, p. 217, STEPHENSEN 1910a, p. 271). A single rather small specimen was taken by the present author W. of Ven, depth ?, on $^{27}/_9$-1925.

Reproduction: A. Literature. The breeding habits are very poorly known. NORDGAARD (1912) off W. Norway observed berried females from early December to early March, planktonic larvae in the latest stage in April, and a bottom stage 4 mm long in August. The whole egg-mass seems to be yellowish-red, while the individual egg was fairly large and purplish in colour. AURIVILLIUS (1898b) off Bohuslän found berried females with eggs in the *Morula*-stage late in November. G. O. SARS (1889) found that eggs with embryos nearly ready to hatch measured fully 2 mm in diameter and described and figured the shortened pelagic development (apparently *Pre-Zoëa* and two *Zoëa*-stages, see also WILLIAMSON 1915, pp. 540—41, figs.).

B. Own remarks. No observations from the Sound or other Danish waters.

Porcellana longicornis (LINNÉ). A *Megalopa* of this species was taken in a bottle-collector W. of Ven, depth 16 m, on $^2/_9$-1939, by the present author.

Reproduction: A. Literature. The breeding habits seem to be almost unknown. LEBOUR (1943) states, from Plymouth, that the species breeds from January to November, the larvae being most abundant in spring and summer. Early eggs were of a deep red colour and measured from $400 \times 310\ \mu$ to $400 \times 325\ \mu$ (WILLIAMSON 1915). Eggs in late stages measured $480 \times 400\ \mu$ (LEBOUR 1943) to $600\ \mu$ in diameter (DUJARDIN 1843). JACKSON (1913a) mentions larvae from the Irish Sea from August (common) to September (rare), and JORGENSEN (1923) found larvae in Northumberland plankton in July (probably the laggards of a batch hatched in spring) and a new batch from July to September or later. — The pelagic larvae, easily recognisable by their extremely long rostrum, have been described and figured by G. O. SARS (1889, *Pre-Zoëa*, first and second *Zoëa* and post-larva), WILLIAMSON (1915, *Zoëa*), and LEBOUR (1943, all stages).

B. Own remarks. No observations on larvae or berried females are available from the Sound, but the *Megalopa* found on $^2/_9$-1939 in our bottle-collectors shows that the larvae may enter the Sound. — In the Copenhagen museum there are found some berried females from Frederikshavn (N.W. Kattegat), depth 26 m, taken on $^{21}/_{7}$-1931 (2 ♀♀ with early eggs, 1 ♀ with somewhat later eggs), on $^{21}/_{7}$-1937 (1 ♀ with early eggs and 2 ♀♀ with somewhat later eggs), and on $^{24}/_{7}$ to $^{12}/_{8}$-1939 (1 ♀ with rather early eggs), and from the area near the Skaw, depth 35 m, taken on $^{6}/_{7}$-1911 (4 ♀♀ with rather early eggs). The number of eggs carried at a time by a single female seems to be small. A rather large female from Frederikshavn taken on $^{21}/_{7}$-1937 had about 425 eggs on its pleopods, and the batch of a small female from the same locality on $^{21}/_{7}$-1931 comprised only about 30 eggs. — In the Copenhagen museum there are also a few larvae from Kattegat plankton taken early in October 1935, and the present author has noted larvae in large numbers in Frederikshavn plankton late in July 1936.

Galathea nexa EMBLETON. Old records from Hellebæk. Not found later.

Reproduction: A. Literature. The breeding habits seem to be unknown. From N. Norway DONS (1915) mentions two finds of berried females in June. G. O. SARS (1889) describes and figures the first *Zoëa* (cf. also WILLIAMSON 1915, as *Galathea dispersa*).

B. Own remarks. The planktonic larvae of *Galathea* taken in the Sound all seem to belong to *Galathea intermedia* (which see). — In the Copenhagen museum there is a berried female with rather early eggs taken N.W. of Hanstholm (S.W. part of Skagerrak), depth 56 m, on $^{31}/_{5}$-1907.

Galathea intermedia LILLJEBORG. Northern and middle parts of the Sound, rare. One specimen was taken by the present author W. of Ven, depth 18—20 m, in August 1936, one specimen off Hellebæk, depth 30 m, on $^{29}/_{7}$-1941, and another specimen in the same locality on $^{2}/_{8}$-1941.

Reproduction: A. Literature. The breeding habits seem to be unknown. AURIVILLIUS (1898b) off Bohuslän found berried females (late eggs) early in August. In plankton from the Sound BJÖRCK (1913) found first and second *Zoëa* from the middle of July to September. The eggs are orange-red in the early stages, later on brownish, and measure 480 × 400 μ when ready to hatch (LEBOUR 1931b). The pelagic larvae have been described and figured by G. O. SARS (1889, second *Zoëa*, first young stage, see also WILLIAMSON 1915), and LEBOUR (1931b, first, third, and fourth larval stages).

B. Own remarks. Planktonic larvae were taken in the Sound off Ven on $^{4}/_{8}$-1928, depth 25—0 m (1 larva, stage III), and off Snekkersten on $^{2}/_{8}$-1928 (1 larva, stage I), $^{2}/_{9}$-1928 (2 larvae, stage II and III), $^{21}/_{9}$-1928 (1 larva, stage I), $^{26}/_{9}$-1928 (3 larvae, stage I), $^{21}/_{10}$-1928 (3 larvae, stage I), and $^{22}/_{7}$-1932 (1 larva, stage I), the season thus being from late July to late October, i. e. somewhat longer than found by BJÖRCK (1913). It is interesting that larvae of this species, the adults of which seem to be rare in the Sound, are met with rather frequently in the plankton and especially in the earliest stages, a fact which seems to indicate that they originate from parents in the neighbourhood. The specimens taken off Hellebæk on $^{29}/_{7}$ and $^{2}/_{8}$-1941 were both berried females with early eggs. — In the Copenhagen museum there are some berried females taken off Frederikshavn (N.W. Kattegat) on $^{12}/_{8}$-1930 (with early and rather early eggs resp.), and larvae from the Kattegat plankton (off the coast of northern Seeland from Sejrø to Tisvilde) taken on $^{3}/_{10}$-1935 (mostly late larvae).

Munida bamffica (PENNANT). Taken in the area round Gilleleje Flak off the northern entrance to the Sound, depth 32 m, in several hundred specimens in 1936 to 1938 (TERSLIN 1940).

Reproduction: A. Literature. The breeding habits seem to be poorly known. Berried females are recorded from northern Norway from the middle of February to late April 1899 (Dons 1915, as *M. rugosa*), from Bohuslän late in July (eggs nearly ready to hatch, Aurivillius 1898b), and off Plymouth from January to April (Plymouth marine fauna 1931). Larvae have been observed in the plankton off W. Norway in May to July (Nordgaard 1912, as *M. rugosa*), in the Irish Sea in April (Jackson 1913a, 1914, stage I–III), off Northumberland in May (Jorgensen 1923), and off Plymouth from January to June (Plymouth marine fauna 1931). Early eggs are orange-red; late eggs are brown and measure 640 to 800 μ in diameter (Lebour 1930). — The pelagic larvae have been described by G. O. Sars (1889, first and last larval stages, first post-larva, good figs., see also Williamson 1915), and Lebour (1930, first and second larva, third and fourth larvae partim, and post-larvae, good figs.).

B. Own remarks. The specimens in the Copenhagen museum taken in the area round Gilleleje Flak include some berried females from $^{9}/_{4}$-1937 (1 ♀ with early eggs), and from $^{29}/_{4}$-1937 (2 ♀♀ with rather early and late eggs resp.). No larvae have been observed in the Sound.

Eupagurus bernhardus (Linné). Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. Nordgaard (1912), Jackson (1913b), and Dons (1915) give some data on the breeding habits. The Pagurids have no copulatory organs; the way in which the fertilisation takes place is unknown, but the sperm is transferred to the female in spermatophores. The process of spawning has not been observed (Jackson 1913b). Berried females are recorded from northern Norway in June to August (Dons 1915), from western Norway in July to August (Nordgaard 1912), from Bohuslän "in March and to the summer" (Aurivilius 1898b), and from the Irish Sea nearly throughout the year (Jackson 1913b). A single batch comprises about 12,000 to 15,000 eggs, and the berried female, when her surroundings are peaceful, often exposes her eggs "and fans them slowly up and down in the water by moving her pleopods" (Jackson 1913b). — The newly spawned eggs are black, nearly spherical, and measure 520 × 600 to 550 × 620 μ in diameter (Williamson 1915), or, off N. Norway, 520 × 660 μ in early and 740 × 790 μ in late stages (Dons 1915). — Pelagic larvae have been observed off Bohuslän in July to August (Aurivilius 1898b), in the Sound in July to September (Björck 1913), off Scotland in June (Williamson 1911), and in the Irish Sea in (February) April to September (Jackson 1913a, b). — The larvae have been described by G. O. Sars (1889, first and last larva, first post-larva, good figs.), partly by Williamson (1911, first *Zoëa*, 1915), and by Gladys Webb (1921, first and fourth larva).

B. Own remarks. Several berried females were taken off Ven early in August 1936 and one berried female off Helsingør on $^{27}/_{4}$-1942. — Planktonic larvae were taken in the Sound off Ven on $^{4}/_{8}$-1928 (3 larvae in the first stage and 11 larvae in the last stage), and $^{17}/_{5}$-1939 (5 larvae), off Snekkersten on $^{19}/_{5}$-1928 (1 larva, first stage), $^{26}/_{9}$-1928 (1 larva, first stage), $^{21}/_{10}$-1928 (1 larva, first stage), $^{11}/_{7}$-1929 (4 larvae in the two last stages), $^{22}/_{7}$-1930 (6 larvae in the two last stages), $^{22}/_{7}$-1932 (1 larva in the first stage and 5 in the last stage, 1 post-larva), and $^{2}/_{8}$-1935 (1 larva, first stage), and off Helsingør on $^{17}/_{9}$-1941 (3 larvae), $^{7}/_{10}$-1941 (2 larvae), $^{21}/_{3}$-1942 (1 larva), $^{10}/_{4}$-1942 (1 larva), $^{27}/_{4}$-1942 (8 larvae in all stages), $^{15}/_{5}$-1942 (1 larva), $^{20}/_{6}$-1942 (1 larva), and $^{5}/_{9}$-1942 (3 larvae). Thus the larval season seems to be from late March to late October, i. e. much longer than found by Björck (1913, see above). — In the Copenhagen museum there are some berried females from Fornæs (W. Kattegat) taken on $^{2}/_{9}$-1907 (3 ♀♀ with early eggs, 4 ♀♀ with rather early eggs, and 3 ♀♀ with rather early eggs), from Randers Fjord taken on $^{26}/_{5}$-1916 (1 ♀ with early eggs), and from Kobbergrunden (near Læsø) on $^{22}/_{3}$-1904 (1 ♀ with early eggs), and larvae from Kattegat plankton from early April (common), and early October (common). Analyses of large numbers of *Eupagurus bernhardus* have been made on populations from Frederikshavn (N.W. Kattegat), depth 10—26 m, from $^{30}/_{6}$ to $^{1}/_{7}$-1937, and from Nissum Bredning (W. Limfjord) $^{2}/_{7}$ to $^{17}/_{7}$-1940, in order to ascertain the number of berried females and the percentage of hermit crabs infected with *Peltogaster paguri*, *Athelges paguri*, and associated with the commensalistic Polychæte *Nereis fucata*:

Locality	Nissum Bredning, depth 0—8 m, $^{2\text{-}15}/_{7}$-1940		Off Frederikshavn, depth 10—26 m, $^{30}/_{6}$-$^{1}/_{7}$-1937	
Specimens with eggs	82	26 %	21	16 %
Specimens without eggs.....	228	73 %	104	79 %
Specimens with *Peltogaster* ..	2	1 %	3	2½ %
Specimens with *Athelges*	0	0 %	2	2 %
Total...	312		130	

The table shows that a large number of females are berried at this time of the year and that the percentage of hermit crabs infected by *Peltogaster* and *Athelges* is very low. No specimens with *Peltogaster* have eggs. Off Frederikshavn I had the opportunity to study the commensalism between *Eupagurus bernhardus* and *Nereis fucata*, and I often found the latter in shells with berried females of *Eupagurus*, the eggs of which were never hurt by the Polychæte. Of the 130 specimens of *E. bernhardus* examined at Frederikshavn, 13 specimens, i. e. 10 per cent, had *Nereis fucata* in their shells.

Eupagurus pubescens (Krøyer). Northern part of the Sound, rare.

Reproduction: A. Literature. Off northern Norway the breeding period is probably from October to April (Nordgaard 1912, Dons 1915). Eggs attached to the pleopods measure 930 to 970 μ (early stages?), in a dwarf-like population 880 to 960 μ (Dons 1915). The larvae occur in plankton off northern Norway in April (Dons). The last pelagic stage has been described and figured by G. O. Sars (1889, cf. also Williamson 1915).

B. Own remarks. No observations from the Sound or other Danish waters.

Anapagurus chiroacanthus (Lilljeborg). Northern part of the Sound, rare.

Reproduction: A. Literature. Berried females are recorded from W. Norway in late June (rather early eggs, Nordgaard 1912), and from Bohuslän in May-July (Aurivillius 1898b). The larvae are known from plankton in the Sound in July to October (Björck 1913), and off Northumberland from the middle of May to September or later (Jorgensen 1923).— The larvae have been described and figured by G. O. Sars (1889, *Pre-Zoëa*, first *Zoëa*, last larval stage, first post-larva, good figs., see also Williamson 1915).

B. Own remarks. Planktonic larvae were taken in the Sound off Snekkersten on $^{2}/_{8}$-1928 (1 early and 1 late larva), $^{2}/_{9}$-1928 (2 larvae, latest stage), and $^{21}/_{10}$-1928 (1 early larva) and off Helsingør on $^{17}/_{9}$-1941 (1 larva), and $^{6}/_{7}$-1942 (1 larva). — The present author observed several berried females off Frederikshavn, depth 26 m, in late July 1936; in the same locality and at the same depth on $^{2}/_{7}$-1937, 63 specimens out of 114 non-infected specimens (i. e. 55

per cent) were in berry, a figure probably comprising all or nearly all the females of the population. In the Copenhagen museum there are some berried females taken off Frederikshavn, depth 22—26 m, in July 1930 (1 ♀ with rather early eggs), and on $^{21}/_{7}$-1931 (1 ♀ with early eggs), and on the eastern slope of Læsø Rende, depth 18 m, on $^{23}/_{7}$-1930 (3 ♀♀ with rather early eggs). In Kattegat plankton (off Tisvilde, N. Seeland) an early larva was observed on $^{4}/_{10}$-1935. — Analyses of larger numbers of *Anapagurus chiroacanthus* have been made on a population from Frederikshavn, depth 26 m, taken on $^{29}/_{7}$-1936, and $^{2}/_{7}$-1937 in order to ascertain the percentage infected with *Peltogaster paguri, Peltogaster sulcatus,* and *Athelges tenuicaudus*:

Date	$^{29}/_{7}$-1936	$^{2}/_{7}$-1937
Specimens without parasites	52—75$^1/_2$ %	114—82$^1/_2$ %
Specimens with *Peltogaster paguri*	8—11$^1/_2$ %	12— 8$^3/_4$ %
Specimens with *Peltogaster sulcatus*	4— 5$^3/_4$ %	9— 6$^1/_2$ %
Specimens with *Athelges tenuicaudus* ...	5— 7$^1/_4$ %	3— 2$^1/_4$ %
Total...	69	138

The infection percentage seems, thus, to be rather high, viz. 24$^1/_2$ and 17$^1/_2$ per cent respectively, and, as in *Eupagurus bernhardus,* I never observed eggs on the pleopods of specimens infected by parasites.

Anapagurus laevis (THOMPSON). Northern part of the Sound, rare.

Reproduction: A. Literature. Berried females are recorded from western Norway in June (rather early eggs), August, and October (several ♀♀ with early, yellowish-red eggs, 1 ♀ with late eggs, NORDGAARD 1912), and from Plymouth in February-April-May-July and August (Plymouth marine fauna 1931). — The larvae do not seem to have been described or figured.

B. Own remarks. No observations from the Sound. — In the Copenhagen museum there are some berried females from eastern Kattegat, depth 44 m, taken on $^{23}/_{7}$-1886 (1 ♀ with early eggs), off Bohuslän, depth 55 m, taken on $^{21}/_{8}$-1885 (1 ♀ with late eggs), and from the Skagerrak, depth 130—140 m, on $^{6}/_{3}$-1903 (1 ♀ with rather early eggs), and $^{19}/_{8}$-1884 (1 ♀ with late eggs). Thus the breeding season seems to be rather long.

General Discussion of the *Decapoda.*

At present bottom stages of 37 species of *Decapoda* are known from the Sound. — For 35 out of these, i. e. 95.5 per cent, the larvae have been described and figured, the two species with unknown larvae being *Spirontocaris spinus* and *Anapagurus laevis.* We know from the Sound the larvae of 20 out of these 35 species, i. e. 57 per cent, all belonging to the category: Species with a long pelagic planktotrophic larval life, viz. ***Crangon crangon,* ***Crangon allmanni, Pontophilus spinosus,* ***Philoceras bispinosus,* **Athanas nitescens,* **Spirontocaris ?gaimardi, Hippolyte varians,* ***Pandalus montagui,* ***Pandalina brevirostris,* **Leander ?adspersus,* **Leander ?squilla,* ***Portunus depurator,* ***Carcinus maenas,* **Cancer pagurus, Hyas* *coarctatus,* **Nephrops norvegicus,* **Porcellana longicornis,* ***Galathea intermedia,* ***Eupagurus bernhardus,* and ***Anapagurus chiroacanthus.* The larvae with two asterisks are recorded from the Sound by Björck (1913) as well as by the present author, those with one asterisk only by the present author, and those without any asterisk by Björck alone.

Although all the larvae found are pelagic and planktotrophic, the length of the pelagic larval life as well as the number of pelagic stages varies considerably from species to species. As a rule the number of pelagic stages is largest within the *Natantia,* with 5 stages in the genera *Crangon, Hippolyte,* and *Leander,* 6 stages e. g. in *Pandalus borealis,* and up to 7 or 8 stages in *Athanas* and *Pandalina* respectively. It is an interesting fact that both *Crangon crangon* with its small eggs (370 to 430 μ in diameter) and *Crangon allmanni* with its much larger eggs (800 × 480 μ in diameter) have 5 very similar pelagic stages, only that the larvae of the latter species are much larger than those of the former. This seems to agree well with the nearly identical mode of development in British and Danish larvae of *Palaemonetes varians microgenitor* in spite of the different egg-sizes in the two areas (cfr. p. 329). It is also curious that *Athanas nitescens,* which is stated by Sars to have rather large eggs and a somewhat shortened pelagic development has nevertheless at least 7 pelagic stages. — Among the *Brachyura* the genera *Portunus, Carcinus,* and *Cancer,* all with early eggs about 320 μ in diameter, have 6 pelagic stages, while the genera *Macropodia, Inachus, Hyas,* and *Eurynome,* with eggs ranging from 360 to 380 μ in diameter, have only 3 pelagic stages. Within the *Homaridae* both *Nephrops* (eggs about 1100 μ in diam.) and *Homarus* (eggs about 1800 μ in diam.) have only 3 (to 4) pelagic stages and a much shortened development. The *Anomura,* finally, have 3 pelagic stages in *Lithodes* (egg about 2000 μ in diam.) and *Porcellana* (egg 325 × 400 μ), and 4 pelagic stages in *Galathea, Munida,* and *Eupagurus* (egg size ranging from 400 to 640 μ in diam.). Thus, as to the *Brachyura, Homaridae,* and, partially, the *Anomura* small eggs seem to be associated with a long pelagic life and several larval stages, while large eggs are associated with a shortened pelagic life and a smaller number of larval stages.

As compared with larvae from the other groups of bottom invertebrates in our main-series the percentage of Decapod larvae is extremely small, viz. off Ven 0.05 per cent, and off Helsingør 0.13 per cent of the whole stock of planktonic larvae, but these rapidly swimming larvae may to some extent have escaped our small nets, the relative frequency, if so, being somewhat larger than appearing from our figures.

According to our rather small collections of Decapod larvae the larval occurrence for the whole Sound is as follows: The first larvae appear in the plankton in (February) March and April, comprising larvae of *Crangon allmanni* and *Eupagurus bernhardus*; the first larvae of *Crangon crangon, Pandalus montagui,* and *Cancer pagurus* appear in May, supplemented in June with larvae of *Leander ?adspersus.* The large number of larval species, however, will not appear until July, when the larvae of *Philoceras bispinosus, Athanas nitescens, Hippolyte varians, Pandalina brevirostris, Carcinus maenas, Hyas coarctatus, Galathea intermedia,* and *Anapagurus chiroacanthus* are added to the species already present. Nearly all the larvae from the July-maximum are still present in August and September, supplemented with the larvae of *Spirontocaris* and *Portunus depurator.* From early October, when the number of larval species is still very high, species as well as specimens will decrease rapidly in number during late October and November, and from early December all the Decapod larvae will be absent from the plankton and do not seem to appear until the spring larvae set in, exceptionally in February, normally in March to April. The distribution of larval species throughout the year calculated on the basis of Björck's (1913) and my own observations is as follows: January

0 sp., February 1 sp., March 1 sp., April 2 spp., May 5 spp., June 6 spp., July 14 spp., August 13 spp., September 13 spp., October 12 spp., November 2 spp., and December 0 sp. —Accordingly the Decapod larvae seem to follow the same rules as were found for the other groups of bottom animal larvae in the Sound plankton, viz. that the largest number of larval species occur in late summer and early autumn, and the minimum occurrence is reached during the actual winter months.

Larvae of *Eupagurus bernhardus* may be found in the plankton during eight months of the year, those of *Crangon crangon* and *Crangon allmanni* during seven months, those of *Pandalus montagui* during six months, and those of *Cancer pagurus* during five months, while larvae of e. g. *Pandalina brevirostris, Portunus depurator, Carcinus maenas, Galathea intermedia,* and *Anapagurus chiroacanthus* are found in the plankton during four months of the year only.

However, the time spent in the plankton by the individual larva is much shorter. In this respect we have no experience from the Sound, but in the literature the spaces of time estimated for the pelagic development for a couple of species are mentioned, viz.: *Crangon crangon* 4 weeks, *Leander adspersus* 4 weeks, *Leander squilla* 4 weeks, *Palaemonetes varians* 15 33 days, *Cancer pagurus* about 2 months, and *Homarus vulgaris* roughly 3 weeks. *Cancer pagurus* with its small eggs and *Homarus vulgaris* with its very large eggs and its shortened development seem to represent the extremes of a long and a short larval life respectively, and in nature the pelagic life of most species of Northern Decapod larvae seems normally to last for about 4 weeks.

While the absolute majority of all other planktonic larvae of bottom invertebrates are phytoplankton-feeders, the Decapod larvae live exclusively, or nearly exclusively, on animal food. Quite young *Zoëae* may feed on Diatoms (*Nitzschia*, Lebour 1928), but the food of most young and all older stages consists of larvae of Echinoderms, Polychaetes, Gastropods, and Lamellibranchs and even of other Decapods. When the food conditions are catastrophic, they will now and then even eat larvae of their own species.

The Decapod larvae have several enemies in the plankton. Thus large numbers of them are eaten by *Medusae* and *Ctenophora* (cfr. pp. 467—471).

12. Echinoderma.

The following authors have contributed to our knowledge of the distribution of the Echinoderm fauna in the Sound: ØRSTED (1844), LÜTKEN (1856—57, 1859, 1871—72 a, 1871—72 b, 1871—72 c), PETERSEN (1889, 1911, 1913, 1914, 1915, 1918), LÖNNBERG (1898, 1899), and MORTENSEN (1924). Finally, BRATTSTRÖM (1941) has given a detailed account of all the Echinoderms found between the Skagerrak and the Baltic with special reference to the Sound. In his fine paper all the topographical and hydrographical factors are considered and thoroughly discussed.

Compared with our knowledge of the larvae of Polychaetes, Prosobranchs, Opisthobranchs, and Lamellibranchs the reproduction and larval stages of the Echinoderms are fairly well known. This is especially due to the fundamental works of Dr. TH. MORTENSEN (1897 a, 1898, 1913, 1920 a, and 1931), who, studying larvae which live in Danish seas, has identified most of them, and has described and figured them in a most beautiful manner. To this should be added the important investigations carried out by CHADWICK (1914), DELAGE (1904), GEMMILL (1912, 1914, 1916), MCBRIDE (1898, 1902, 1903, 1907, 1914, 1918), MASTERMAN (1902), NARASIMHAMURTI (1933), OLSEN (1942), J. and S. RUNNSTRÖM (1919), S. RUNNSTRÖM (1924, 1927 b), RUSSO (1892), M. SARS (1844, 1846), SHEARER, MORGAN and FUCHS (1913), and THÉEL (1892, 1902). Thus their reproduction biology is already known in broad features, and the larvae of 26 of the 32 species of Echinoderms whose bottom stages are known from the Sound had been described in more or less detail and figured before the present paper was finished.

As regards most species we have therefore considered it unnecessary to figure the larvae again; on the whole our investigations of the Echinoderm larvae in the Sound have been much less intensive than of the invertebrate groups whose larvae were poorly known. The larvae of the main series have, however, been carefully determined, and such larvae as failed to appear, though their adults were of common occurrence, have been zealously sought for.

Astropecten irregularis (PENNANT). Northern part of the Sound, rather common.

Reproduction: A. Literature. METSCHNIKOFF (1869) figures a larva which he refers to *Astropecten aranciacus* in a later paper (1885); it has also been reared by DRIESCH (1897). MORTENSEN (1897 a), who records the larva as *Bipinnaria Metschnikoffii,* seems to accept this supposition, and refers a larva figured by JOHANNES MÜLLER (1853) as "Bipinnaria von Helsingør und Ostende" to the genus *Astropecten*. HÖRSTADIUS (1926, 1939) describes similar stages of *Astropecten aranciacus.—A. irregularis* is known to breed near Bergen in the summer (S. RUNNSTRÖM 1927 a).

B. Own remarks. All larvae referred in the literature to *Astropecten* have a characteristic appearance, having short processes and no *Brachiolaria* stage. Larvae of this type, all belonging to the same species, are found in our samples from the Sound. Since, furthermore, only three genera of Asterids found in the Sound have pelagic larvae, viz. *Asterias* (*Brachiolaria* larvae), *Luidia* (very large, characteristic larvae, see below), and *Astropecten*, the larvae in question should decidedly be referred to *Astropecten irregularis*. Such larvae were secured off Ven on: $^{17}/_{10}$-36; $^{23}/_{7}$-37; $^{18}/_{4}$-38; $^{11}/_{9}$-38; and $^{17}/_{6}$-39; thus occasional specimens occur from the early spring to the late autumn. Only seven specimens were observed, and one specimen only, taken on $^{23}/_{7}$-37, had begun to develop a bottom stage. The main series for a whole year taken off Helsingor contained only a single larva of this species, viz. a young specimen collected on $^{17}/_{8}$-1942.

Luidia sarsi Düben and Koren. Öretvisten, rare. Not taken during the last 15 years.

Reproduction: A. Literature. Larva described by M. Sars (1835), and later referred by Ludwig (1895) to *Luidia sarsi*. Mortensen describes (1897 a) its characteristics in detail and figures (1924, after Johannes Müller) the late-stage larva. Garstang (1894) figures what he takes to be a young planktonic larva of this species. Mortensen (1913) states that Garstang's larva belongs to *L. ciliaris*. Nordgaard (1912) found larvae of *L. sarsi* in the plankton off Bergen in November, February, and March, with a pronounced maximum in the two latter months. Tattersall and Sheppard (1934) give a list of all the records in the literature from English waters, summarise the characteristics which distinguish the *Luidia sarsi* larva from that of *Luidia ciliaris*, and give good figures of both of them. On the basis of several observations the same authors are able to confirm the surprising observations (Koren and Danielsen 1847, and M. and C. Delap 1907) "that, at the time of metamorphosis, the larval arms and preoral lobe, in fact all the larval body which has not been incorporated into the starfish rudiment, is cast off. The discarded larval body swims away and may go on living for some time, as long as three months . . .". This, however, does not apply to the closely related *Luidia ciliaris*. — Søren Jensen, Johansen and Levinsen (1903) record the larva of *L. sarsi* found in plankton derived from the following localities in Danish waters: Skagens Rev, November—December 1899 (common), January to April 1900 (rare), December 1900 to January 1901 (rare); Læso Rende, December 1899 (rare); Anholt Knob, March 1901 (rare), and Schultz Grund, April 1900.

B. Own remarks. In spite of its very characteristic features and large size ($2^1/_2$—$3^1/_2$ cm) this larva has never been observed in the Sound. The above data from other Danish waters seem to show that the larva is rare in the inner parts of these waters.

Henricia sanguinolenta (O. Fr. Müller). Northern part of the Sound, not very common.

Reproduction: A. Literature. M. Sars (1844) has described and figured the brood-protection and non-pelagic larvae of this species. Masterman (1902) has made a careful study of the brood-protection. Spawning at St. Andrews in February to April, near Norway in the spring. The mother animal, which forms a breeding room between its arms, is attached to the under surfaces of rocks and stones. The older larvae, hatched from the egg membrane, will often rotate in the breeding room and adhere to the substratum. If the mother animal is removed, the larva will continue its development and metamorphose, and eggs and larvae washed out from the breeding room will as soon as possible attach themselves to a substratum and remain there until metamorphosis. The barrel-shaped orange-coloured larva is similar to those of *Solaster endeca* and *S. papposus*, and habitually to that of *Psolus phantapus*. Gemmill (1916) states that at Millport the species may reproduce by pelagic eggs and larvae without brood-protection. These eggs and the embryos are, however, of precisely the same type as those protected by the mother, and — though occasionally pelagic — take no food from the plankton.

B. Own remarks. Larvae of this barrel-shaped, orange-red type are known from our summer samples of 1937 and 1939. When reared in aquaria, they proved to belong to *Psolus phantapus* (which see), but if they are not reared, it seems very difficult to identify them.

Solaster endeca (Linné). Northern part of the Sound, rather common. Young specimens most frequent.

Reproduction: A. Literature. Spawning habits and larvae described and figured by Gemmill (1912). Breeding season (at Millport and Bergen) March to April (Gemmill l. c., S. Runnström 1927a, Nordgaard 1912). An animal spawns several times a week. About 3000 eggs were shed during the main spawning, which lasted for two hours. The eggs, yolky and orange-coloured, are shed singly and float at the surface of the water. "A larval mouth is never formed, and the store of food contained in the egg has to last until the end of metamorphosis" (Gemmill l. c.). The larvae hatch 6 days after fertilisation, and are afterwards pelagic for about 12 days. They are ciliated, orange-red, barrel-shaped, with three larval arms around the sucker, and for about two or three days rotate on their own axis at the surface. Later on they descend to deeper water layers, and finally they fix themselves to the substratum to metamorphose.

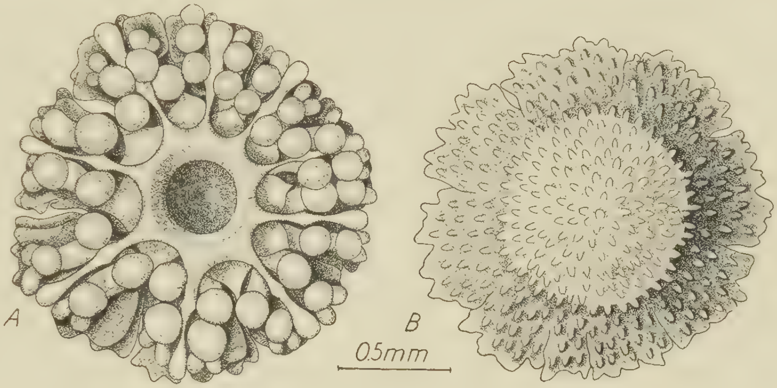


Fig. 191 A-B. *Solaster endeca* (Linné), just metamorphosed bottom stage. — *A*. From the ventral, and *B*. From the dorsal side. From a bottle-collector exposed off Ven at a depth of 16 m from $^{27}/_{5}$ to $^{20}/_{7}$-1941 (drawn from life on $^{21}/_{7}$).

B. Own remarks. Like the other lecithotrophic larvae (*Psolus phantapus, Henricia sanguinolenta*, cf. pp. 360 and pp. 344) the larva of *S. endeca* is very difficult to identify. Larval arms of the type figured by Gemmill as characteristic of this species have, however, never been observed among the barrel-shaped, orange-coloured larvae found off Ven and Helsingør (which were partially reared to *Psolus phantapus*). Thus, in spite of the rather common occurrence of the adults in the Sound the larvae has not been found in our samples, and it is quite probable that small numbers of larvae just ready to settle drift into the Sound from the Kattegat. In a bottle-collector exposed off Ven from $^{27}/_{5}$-41 to $^{20}/_{7}$-41 at a depth of 16 m, a single, just metamorphosed young of *Solaster endeca* (fig. 191 A–B) was found. The colour was carmine and the diameter was about 1650 μ. To judge from the size of this young bottom stage and from the season at which the bottle-collector was exposed, it seems justifiable to conclude that the few larvae occasionally present in the Sound occur in the plankton in June-July, i. e. at the same time as the larva of *Psolus phantapus*, with which they may easily be confused on a cursory examination. Adults with ripe sexual organs seem, at any rate, to be rare in the Sound.

Solaster papposus (Linné). Northern part of the Sound, rare. Hardly attains sexual maturity in the Sound.

Reproduction: A. Literature. Spawning, larval development, and larval stages quite similar to those of the preceding species (Gemmill 1912), from which the larva can hardly be distinguished. Chadwick (1914) was unable to distinguish between the larvae of these two species in Port Erin plankton. Spawning at Trondhejm in April to June. Eggs yellowish-white, seem to float in the water (Nordgaard 1912). According to Chadwick (1914, p. 475) the egg is of an orange colour.

B. Own remarks. The larva is unknown from the Sound.

Asterias rubens Linné. Very common throughout the Sound.

Reproduction: A. Literature. Larva described i. a. by Hensen (1863), M. Sars (1863), and Greeff (1876), and identified by Mortensen (1897). It has been reared to the young bottom stage by Gemmill (1914). He states (l. c.): breeding season in different localities within the months March to September, varying from place to place. Spawning at Millport in April to June-July, varying from year to year. Spawning in nature "probably occurs at least twice in the same starfish in a single season". Sperms suspended in the water induce spawning in ripe females. Eggs shed singly and freely in the sea. "A particular starfish measuring $5^1/_2$" across disc and arms was estimated to have extruded over 2,500,000 eggs at a single period" (i. e. 2 hours). The eggs are 160—190 μ in diameter with an egg membrane 7.5 μ thick. — The larva has a typical *Brachiolaria* stage and attains a size of 2 mm. Mortensen (1913) is of opinion that the larva of *Asterias rubens* differs from that of *A. glacialis* in having only 2—3 papillae on either side of the sucking disc at the bases of the brachiolarian processes, while the sucking disc in *A. glacialis* is surrounded by a complete ring of small papillae. As, however, the full-sized larva of *A. glacialis* is still undescribed, the difference between the larvae of the two species in question is at present only little known. — Mortensen (1924) states that the larva is very common in the Kattegat and the Belts, but not in the eastern Baltic, and that the breeding season varies considerably with the locality (the Limfjord: May to July; the western Baltic: August to September). Søren Jensen, Johansen, and Levinsen (1903) record larvae of this species from Thyborøn, Skagens Rev, Læsø Rende, Anholt Knob, and Schultz Grund, all from July and August. Mortensen (1924) assumes that adult animals now and then occurring in the inner part of the Baltic have been carried there with "drift-larvae".

B. Own remarks. As mentioned above not all stages of this larva can be distinguished with certainty from that of *A. glacialis*. As, however, *A. rubens* is far more abundant in the Sound than the latter species, which is extremely rare, I have referred all the larvae of this type to *A. rubens*. In spite of the common occurrence of adult specimens, *Asterias* larvae are not met with in large numbers in the Sound. Compared for instance with the western Limfjord or Frederikshavn, where the larvae are met with in large numbers in June-July, the number of larvae in the Sound is not very considerable, but on the other hand the larval season seems to be rather long. Larvae are known from the Sound from the following dates, taken near Ven: $^{24}/_{7}$-37; $^{12\text{-}14}/_{8}$-37; $^{9}/_{10}$-37; $^{10}/_{5}$-38; $^{6}/_{6}$-38; $^{18}/_{6}$-38; $^{1}/_{7}$-38; $^{17}/_{7}$-38; $^{21}/_{7}$-38; $^{10}/_{4}$-39; $^{17}/_{5}$-39; $^{4}/_{6}$-39; $^{3}/_{7}$-39; $^{15}/_{7}$-39, and $^{19}/_{8}$-44; and near Helsingor on: $^{8}/_{7}$-41; $^{11}/_{7}$-41; $^{14}/_{9}$-41; $^{4}/_{6}$-42 (quite young); $^{20}/_{6}$-42; $^{6}/_{7}$-42; $^{18}/_{7}$-42, and $^{25}/_{7}$-42. Thus the season extends from early April to early October with a maximum in May-June-July. The first *Brachiolaria* stages were observed in early June, and the first bottom stages of the larvae early in July. Young, just metamorphosed bottom stages were found in large numbers at Hittarps Rev, 25 m, on $^{28}/_{7}$-41, and off Hellebæk, 25 m, on $^{4}/_{8}$-41. Young metamorphosed bottom stages occurred in bottle-collectors near Ven on $^{23}/_{8}$ to $^{2}/_{9}$ 1939, on $^{18}/_{8}$-40, and on $^{17-20}/_{7}$-41.

Adults of two different orders of magnitude seem to occur in the Sound, viz. medium-sized specimens (10 to 15 or 20 cm across disc and arms) which are abundant at depths of 10 to 20 m, and gigantic specimens (40—50 cm across disc and arms) which occur at greater depths (about 30—40 m, cf. also Brattström 1941 p. 168). Judging from the conditions normally prevailing in the Sound it might be expected that the medium-sized specimens living at smaller depths would spawn earlier than the large specimens occurring at greater depths, and ripe medium-sized specimens are indeed common in May-June. An examination of large specimens from a depth of 30—40 m late in June and July showed that they were astonishingly lank and with small, even reduced, gonads. As the last large larvae of *Asterias rubens* occur in October, the spawning must accordingly be completed in September, and it seems not reasonable to assume that specimens which have small gonads as late as early August will be able to spawn about one month later. It seems justifiable, therefore, to assume that the large specimens living in deep water in the Sound are senile animals, which, after ceasing to produce sexual products, have continued their vegetative life and have used all their surplus of nourishment to increase in size, not to reproduce. A similar case was probably observed by Mortensen (1920 p. 146) in another Echinoderm, *Brissopsis lyrifera*, in the Gullmar Fjord. In the inner part of this fjord he observed a number of unusually large specimens of *Brissopsis* in which the genital organs were quite black without the slightest indication of sexual products. Mortensen adds: "I have no doubt that these large specimens were really quite senile and had passed the age of sexual reproduction".

Asterias (Leptasterias) mülleri Sars. Northern part of the Sound, rather common locally.

Reproduction: A. Literature. M. Sars (1844 and 1846) has described the brood protection in this species, in which the mother animal, just as in *Henricia sanguinolenta*, forms a breeding room between the under surface of the disc, the arms, and the substratum. Here the eggs and young, 50 to about 110 in number, develop, and the mother animal does not feed before the brood leaves the breeding room as fully developed young bottom stages. Masterman (1902) states that the brood instinct is more deeply rooted in *A. mülleri* than in *Henricia*. The young in the breeding room of *A. mülleri* are so closely entangled that they can only be separated from each other by force. Accordingly the eggs and larvae will normally never be found to be planktonic. When the mother animal is removed by force, the embryos will continue their development in the normal way. — Breeding season near St. Andrews: November to December (Masterman 1902), near Norway: March to April (Sars 1846), in Danish waters: the winter months (Mortensen 1924).

B. Own remarks. Specimens with young have never been observed in our collections.

Asterias (Marthasterias) glacialis Linné. Kullen, mostly rare.

Reproduction: A. Literature. Breeding near Bergen in summer (S. Runnström 1927a). Only younger larvae have been reared and figured under natural conditions (Russo 1892, Mortensen 1913, Chadwick 1914, Pl. 1. fig. 10, and Gemmill 1916), while Delage (1904), by artificial parthenogenesis, obtained fully developed larvae. See also the remarks under *Asterias rubens*.

B. Own remarks. Larvae of this species, at any rate the older stages, which are pelagic with a *Brachiolaria* stage, cannot be distinguished with certainty on the basis of the descriptions from those of *A. rubens,* to which all the larvae of this type found in our samples have been referred.

Ophiothrix fragilis ABILDGAARD. Southwards to Ven, rather common locally.

Reproduction: A. Literature. JOH. MÜLLER (1852) has identified the larva, which has been reared to the young bottom stage (at Plymouth) by MCBRIDE (1907). The eggs are opaque, yolky, yellow, and measure 100 μ in diameter. Larvae arising from natural fertilisation develop more quickly (according to MCBRIDE l. c.) than those obtained by artificial fertilisation. Some larvae have been figured by CHADWICK (1914, fig. 32—36). MORTENSEN (1897a and 1931) gives some beautiful figures of the pelagic larva, which has very long, characteristic postero-lateral arms, each with 2—3 dark transverse bands. Larvae reared in the Plymouth aquaria took 26 days or somewhat less to pass from fertilisation to metamorphosis (MCBRIDE 1907). KERR (1912) has likewise figured the larva. SMITH (1938) has described "false incubation" in this species. He found young specimens in the genital bursae of the adults, where they have, no doubt, arrived after metamorphosis.

B. Own remarks. The characteristic larvae were present in our samples from Ven taken on: $^{26-27}/_{9}$-36; $^{17}/_{10}$-36; $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{13}/_{7}$-39, in July-August 1940 and on $^{19-21}/_{8}$-1944, and from Helsingor taken on $^{7}/_{10}$-41. Near Frederikshavn they are met with every summer in the month of July, and at the end of July, 1935, males as well as females spawned here in glass dishes. Young as well as older larvae are present from the Sound, but only one of them contained a young bottom stage ($^{9}/_{10}$-37), and it must be assumed that most of the larvae secured are "drift larvae" from the Kattegat water, which is pressed into the Sound during the first westerly gales in the autumn.

Ophiocomina nigra (ABILDGAARD). N. of Ven and off Knähaken, occasional specimens.

Reproduction: A. Literature. Pelagic larvae figured by GRAHAM KERR (1912), young larvae described by MORTENSEN (1913) and CHADWICK (1914 fig. 38), and late-stage larvae figured by MORTENSEN (1931). NARASIMHAMURTI (1933) has described the whole larval development and the metamorphosis at Plymouth. The egg is 96 to 100 μ in diameter. The larva has a pair of ciliated lobes at the base of each postero-lateral arm, which makes it easily recognisable. — Spawning of brownish eggs, 96 μ across, at Bergen in July (NORDGAARD 1912).

B. Own remarks. This larva is found in plankton in the Sound in the late summer. In our samples taken near Ven it is present from the following dates: $^{21}/_{8}$-36; $^{9}/_{8}$-37; $^{12-13}/_{8}$-37; $^{12}/_{9}$-37; $^{9}/_{10}$-37, and $^{16-19}/_{8}$-44. In the years 1938 and 1939 no larvae were secured in spite of careful investigations. A large larva without any bottom stage inside was found off Helsingor on $^{5}/_{9}$-42. This seems to show that the larvae are typical "drift larvae" which in certain years are carried by strong currents from the Kattegat, where the species is abundant in the northern parts, into the Sound. There is, however, a possibility that the species has not spawned at all in 1938 and 1939. In the summers of 1940 and 1941, also, this larva was absent from the rather few plankton hauls made in the Sound. In several of the larvae collected on $^{9}/_{8}$-37 the bottom stage had begun to develop; it seems quite probable that they may metamorphose and commence a vegetative bottom stage in the Sound, only reaching the stage of maturity in years in which conditions are especially favourable.

Ophiopholis aculeata (O. FR. MÜLLER). Northern part of the Sound, common at great depths.

Reproduction: A. Literature. Fewkes (1886) has reared the young larvae and has (1887) described and identified the older larvae from N.E. America. Mortensen (1897a) discusses the earlier literature, gives good figures of the larva, which he has never seen alive, and records it from: "Skagerak, the Kattegat and the Sound at Hveen. In Danish seas in April-May". Breeding at Bergen in March (Sven Runnström 1927a). Later Mortensen (1920a) reared these larvae to young pelagic stages at Trondhejm; they were, however, too young to enable him to ascertain their identity. The most characteristic feature of the pelagic stage is the short but distinct forward-directed process on each of the transverse rods. Haakon Olsen (1942) describes in detail the whole development from Bergen: Breeding season from the middle of April to the last part of May. Ripe animals placed in a heated laboratory will spawn after a quarter of an hour. The males mostly spawn first. The spawning takes several minutes, and all the eggs are fertilised. The female probably lays all her ripe eggs at the same time. Diameter of the globular egg about 0.1 mm; it is of a reddish, yellow or yellowish-brown colour. The full-grown pluteus (about 30 days after fertilisation at 8° C.) agrees in all essentials with that already referred to this species by Mortensen (1897a), and the characteristic processes on the transverse rods seem to be so good a character that the larva can easily be recognised in the plankton.

B. Own remarks. According to the figures of Mortensen (l. c.) and Olsen (l. c.) it would seem that the larvae occurring in the Sound can only be confused with those of "*Ophiopluteus compressus*". We were aware of this during the investigations and consequently examined the transverse rod in all the larvae of this type, which all proved to belong to *O. compressus*, not to *Ophiopholis aculeata*, the larva of which has never been taken in our samples. This fact seemed peculiar, since a three years' main series was at hand from Ven; probably, however, the larvae occurred in the northernmost part of the Sound at greater depths than those examined off Ven. When, therefore, the main series from 30—0 m off Kulla Gunnarstorp was secured in 1941—1942, we expected to find the larva and looked carefully for it all the year round — but in vain. The absence of this larva seems difficult to explain, especially since the adults are of common occurrence and may be found as far southwards as Flintrännan. Probably the stock of adults in the Sound is recruited mainly from the Kattegat, from a rather small number of older larvae just ready to metamorphose and settle (cf. pp. 394—396).

Amphiura filiformis (O. Fr. Müller). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. The larva, *Ophiopluteus mancus*, has been described and figured by Mortensen (1901), and by Chadwick (1914, fig. 20—31). The young larvae have been reared and the pelagic larvae identified by Mortensen (1920a), who (1931) gives beautiful figures of larvae in different stages of development. The males are the first to spawn and induce spawning in the females. All the eggs and sperms were discharged at the same time on a single day. Young larvae were reared, and their later stages could be observed in the plankton (Mortensen 1920a). The larva is very characteristic by having no postero-dorsal arms, and the tips of the arms have orange or red pigment. According to Mortensen (1924) it is found in the Danish waters during the whole summer until October. See, however, also the remarks under *A. chiajei*.

B. Own remarks. Among the Echinoderm larvae of the Sound that of *A. filiformis* is by far the most abundant, possibly in connection with that of *A. chiajei* (which see). It occurs every year from August to October, with an absolute maximum in September-October. In these months up to 380 larvae were secured in ten vertical hauls. A single larva was met with as late as $^{6}/_{1}$-38, but from this date till late in July larvae were entirely absent from the plankton in the Sound. In August only young larvae were found, and the first larvae with bottom stages developed inside were met with in September. The young August larvae, which must be supposed to originate from parents in the Sound itself or from neighbouring areas, are far too small in number to be the only cause of the sudden maximum in September-October, which consists almost exclusively of older larvae and larvae with young bottom stages inside. The greater number of these larvae originate, no doubt, from Kattegat parents and have been carried into the Sound by the autumnal currents. The greater part of the *Amphiura filiformis* population in the Sound must, therefore, be supposed to be recruited from the Kattegat. The large autumn maximum characteristic of larvae of this species was ascertained off Ven in 1936, 1937, 1939, and 1941, but failed to appear in 1938. In this year the maximum (only 60 larvae in ten samples) occurred as early as $^{17}/_{7}$, while the September-October plankton contained only 1—16 larvae in ten samples. The causes of this sudden absence of the normal maximum of this species will be discussed on pp. 380—381 (cf. also the following species). Young metamorphosed bottom stages were taken in bottle-collectors off Ven on $^{23}/_{8}$-39; $^{2}/_{9}$-39 (numerous); $^{21}/_{10}$-39, and $^{12}/_{8}$-40, and off Helsingør on $^{14}/_{9}$-41; $^{25}/_{10}$-41; $^{11}/_{11}$-41; $^{17}/_{8}$-42, and $^{5}/_{9}$-42.

Amphiura chiajei Forbes. Rather common in the northern and middle parts of the Sound.

Reproduction: A. Literature. Mortensen (1920a) states that at Kristineberg this species begins to breed by the middle of September, i. e. at the time when *A. filiformis* has just finished its breeding season in the same locality. Since in specimens breeding in aquaria the sperms were inactive, no fertilisation took place, and plankton hauls from October contained only the larvae which he had just identified as belonging to *A. filiformis*. This implies either that the larva of *A. chiajei* cannot be distinguished from that of *A. filiformis* or that no larvae of *A. chiajei* were at all present in the samples. Thus the larva of *A. chiajei* still remains unknown.

B. Own remarks. According to our experience from the Sound there seems to be a very close resemblance between the larvae of *A. chiajei* and those of *A. filiformis*. The adult *A. chiajei* is so common in the Sound that the larvae of this species, which according to the size of the eggs are pelagic, must be assumed to occur in our four years' samples from Ven and Helsingør. It is not very probable that such a common species should not have produced any larvae during four years, three of which were consecutive years. However, no larvae are found in our samples apart from those referred to *A. filiformis*, which may be the larvae of *A. chiajei*, and accordingly the larval stages of the two species must be so similar that they can hardly be distinguished from each other. If so, the above observations on the larvae of *A. filiformis* in the Sound will also apply to the larvae of *A. chiajei*. But since *A. filiformis* is by far the most abundant of these two species in the Sound, and the maximum of large *Amphiura* larvae in the Sound reaches its culmination by the middle of September (i. e. at the time when *A. chiajei* seems to begin its breeding, at any rate at Kristineberg) the larvae of *A. chiajei* will hardly influence the total maximum.

Amphipholis squamata (D. Ch.). Known from: Hellebæk; $3^{1}/_{2}$ miles NNW. of the Lappegrunden lightship, and off Landskrona. Probably often overlooked.

Reproduction: A. Literature. De Quatrefages (1842) was the first to note the viviparity of this cosmopolitan species. Later on several authors, e. g. Krohn (1851), M. Schultze (1852), Ludwig (1882), Fewkes (1887), and Bernasconi (1926) have studied the embryonic development in detail. Metschnikoff (1870) found the species to be hermaphroditic, and Russo (1893) gives detailed figures of the developing embryos and their structure. Embryos at all stages of development are seen simultaneously in nearly all specimens. These embryos undergo a much reduced development very different from that of the *Ophiopluteus* type met with in species with pelagic larvae, and the young leave the mother animals in the crawling stage, when they have reached the shape of the adults.

B. Own remarks. I have been able to examine four large specimens (preserved in alcohol) kept in the Copenhagen museum. They were all taken in the inner Danish waters, three of them in the Sound, and they all measured about 3 mm. across the disc. A specimen taken SE. of Trindelen (Kattegat), 35 m, on $^{17}/_{5}$-1923, contained two embryos, both in the same bursa; in the younger specimen the disc had just formed, the older was nearly ready to hatch. A specimen taken $3^{1}/_{2}$ miles NNW. of the Lappegrunden lightship on $^{19}/_{5}$-1923 (depth unknown) contained not the slightest trace of embryos (though it was well preserved). Two specimens taken off Hellebæk (date and depth unknown) contained four and six embryos respectively — all of different sizes, but of the same shape as the adults. — These few examples show that the breeding intensity is small (2 to 6 embryos only at the same time in a single mother animal) as compared with other marine viviparous invertebrates in our seas, i. e. *Littorina saxatilis* (on an average 60 to 900 embryos at the same time in a female), and *Hydrobia jenkinsi* (on an average 22 embryos at the same time in each female). Further, it is evident that the embryos in *A. squamata* are fertilised and developed singly — not in "crowds" as for instance in *Littorina saxatilis.* Finally the fact that young as well as old embryos have been found at the same time in the bursae of all three specimens examined seems to suggest that breeding takes place during a rather great part of the year, probably all the year round; this is in good agreement with our knowledge of the breeding period known for other viviparous species in the Sound.

Ophiura texturata Lamarck. Rather common in the northern and middle parts of the Sound.

Reproduction: A. Literature. The pelagic larva, easily recognisable by its fenestrated postero-lateral arms and its large, green stomach, has been identified and figured by Mortensen (1897 a) from the Limfjord, in the inner part of which *Ophiura texturata* is the only *Ophiura* found, and where its larvae occur throughout the summer in all stages of development. Chadwick (1914 fig. 43) figures a larva from the Port Erin plankton. Mortensen (1931) also gives a beautiful figure of the living larva.

B. Own remarks. In spite of the common occurrence of this Ophiurid both north, east, and south of Ven, the larva has never been found in our plankton samples off Ven or off Helsingør. From the beginning of our investigations we have looked for this larva, which I know so well from the Limfjord and the Isefjord, but in vain. The absence of this characteristic larva in the Sound may probably be accounted for in the same way as the absence of the larva of *Ophiopholis aculeata* (which see).

Ophiura sarsi Lütken. Northern part of the Sound, not common.

Reproduction: A. Literature. Mortensen (1897 a and 1931) figures and describes a larva: *Ophiopluteus compressus,* with characteristic flat transverse rods, and with faint purplish-black spots on the postero-lateral and the postero-dorsal arms. He adds (1931, p. 36) "I have suggested that it may be the larva of *Ophiura sarsi,* but it is merely a suggestion; *Ophiura robusta* or *Ophiocten sericeum* might equally well come into consideration". Since then, however, Thorson (1934) has identified what he supposed to be the larval stages of *O. robusta* and *Ophiocten sericeum* in East Greenland — the former, however, by calculation of probabilities only — and according to this it seemed most justifiable to refer the *Ophiopluteus compressus* larva to *Ophiura sarsi.*

B. Own remarks. The larva is recorded (by Mortensen 1897 a) from the Skagerrak, the Kattegat, and the Sound from April and May, and in our samples, also, this larva (besides a few larvae of *Psammechinus miliaris*) is the only Echinoderm larva occurring as early as April. From this month it is met with regularly during the whole spring and early summer. Up to 1600 larvae in a main series have been found, but normally only 10—20 larvae occur in ten samples. Even as late as October-November some few specimens may be present in the plankton, though the number decreases rapidly towards the end of the summer. Thus the larva in question is very common in the Sound. It is astonishing, however, that young, newly hatched larvae are abundant especially in the spring, while older larvae just ready to metamorphose seem to be rare. Thus out of the 260 larvae of *Ophiopluteus compressus* examined in the Ven plankton only one was seen with the bottom stage inside, ready to metamorphose. It must therefore be taken for granted that the larvae are produced in the Sound or its nearest vicinity, and that the parents may be looked for among species which are abundant in the Sound. However, *Ophiura sarsi* is rather rare in the Sound, and therefore hardly the parent of this species.

Hence there is hardly any doubt that the larva which was identified by Thorson (1934) in Greenland as belonging to *Ophiura robusta* should be referred to *Ophiura sarsi.* This assumption is supported by the fact that adult specimens of *Ophiura robusta* are very abundant in the Sound, where the "*Ophiura robusta* larvae" from East Greenland have never been met with. While the identification of the *Ophiocten sericeum* larvae in East Greenland must be regarded as beyond doubt, the "*O. robusta* larva" was rather abundant in Scoresby Sound (samples only from July-August 1933) in a place where *O. robusta* was the only Ophiurid of frequent occurrence. Since the larvae, too, were likewise rather frequent, I did not hesitate to refer them to *O. robusta. Ophiura sarsi,* however, though not of common occurrence, is also known from these parts of Scoresby Sound, and considering the conditions prevalent in Danish waters it is likely that the Scoresby Sound larvae should be referred to *O. sarsi,* not to *O. robusta,* while the larva of *O. robusta* is that hitherto recorded as *Ophiopluteus compressus.*

Thus the larva of *Ophiura sarsi* has never been met with in our main series, and the reproduction of this species is therefore unknown from the Sound.

Ophiura robusta (Ayres). Common in the northern and middle parts of the Sound.

Reproduction: A. Literature. According to the remarks given above for *Ophiura sarsi,* it seems justifiable to refer the larva of *Ophiopluteus compressus,* described and figured by Mortensen (1897 a and 1931) and Chadwick (1914 figs. 44—45), to *Ophiura robusta.* As mentioned above this larva is easily recognisable owing to its characteristic flat transverse rods and the faint purplish-black spots on the postero-lateral and postero-dorsal arms.

B. Own remarks. As might be expected from the frequency of the adults, this larva plays an important part among the Echinoderm larvae of the Sound. In our main series they are present from a great number of dates, viz. from Ven: $^{1}/_{11}$-36 (3 spms.); $^{14}/_{11}$-36 (1 spm.); $^{18}/_{4}$-37; $^{2}/_{5}$-37; $^{23}/_{5}$-37; $^{6}/_{6}$-37; $^{9}/_{8}$-37 (1 spm.); $^{21}/_{8}$-37 (1 spm.); $^{12}/_{9}$-37 (1 spm.); $^{23}/_{10}$-37 (1 spm.); $^{14}/_{11}$-37 (1 spm.); $^{3}/_{4}$-38 (28 spms.) ;$^{18}/_{4}$-38 (16 spms.); $^{10}/_{5}$-38 (60 spms.); $^{6}/_{6}$-38; $^{18}/_{6}$-38 (16 spms.); $^{29}/_{4}$-38 (4 spms.); $^{10}/_{4}$-39 (12 spms.); $^{17}/_{5}$-39 (70 spms.); $^{4}/_{6}$-39 (30 spms.); $^{17}/_{6}$-39 (4 spms.); $^{3}/_{7}$-39 (8 spms.); $^{15}/_{7}$-39 (6 spms.) and $^{19}/_{8}$-44, — and from Helsingør: $^{8}/_{7}$-41; $^{11}/_{7}$-41; $^{17}/_{9}$-41 (2 spms.); $^{7}/_{10}$-41 (4 spms.); $^{25}/_{10}$-41 (6 spms.); $^{11}/_{11}$-41 (2 spms.); $^{10}/_{4}$-42 (1600 spms.); $^{27}/_{4}$-42 (208 spms.); $^{15}/_{5}$-42 (120 spms.); $^{4}/_{6}$-42 (800 spms.); $^{20}/_{6}$-42 (100 spms.); $^{6}/_{7}$-42 (100 spms.); $^{18}/_{7}$-42 (30 spms.); $^{25}/_{7}$-42 (10 spms.), and $^{5}/_{9}$-42 (40 spms.).

Thus the main season of occurrence is April to June, and during this season only young and half-grown larvae are found, but never with a bottom stage formed inside. The few metamorphosing larvae met with are recorded from the end of July, August, and September. Young bottom stages were found in bottle-collectors off Ven, 16 m, on $^{17\text{-}20}/_{7}$-41. While Echinoderm larvae nearly always had empty stomachs when examined, some of the *Ophiura robusta* larvae from $^{20}/_{6}$-42 (taken off Helsingor) had small phytoplankton organisms in their stomachs, which were densely filled with these strongly coloured green cells measuring 5 μ in diameter.

Ophiura affinis LÜTKEN. Northern part of the Sound. Rather common locally.

Reproduction: A. Literature. A larval stage described by JOHANNES MÜLLER from the Adriatic Sea (1853), and another by MORTENSEN (1920a) from Kristineberg, later figured by the same author (1924), may be referred to this species. However, according to MORTENSEN the identity must be regarded as rather doubtful. According to the figure the larva is pelagic, but only the two postero-lateral arms seem to develop.

B. Own remarks. Thus on account of its milky, opaque colour the larva closely resembles dissolving abnormal larvae of *Amphiura filiformis*, with which it may have been confused in the Sound plankton. If so, however, it is only of sparse occurrence in the Sound plankton, for only a very small number of such "abnormal *Amphiura* larvae" have been met with.

Ophiura albida FORBES. Northern and middle parts of the Sound, extremely common.

Reproduction: A. Literature. The pelagic larvae have been identified by HENSEN (1886). MORTENSEN (1897a) describes and figures the larva of this species, and states that it is especially common in August-September (in the Limfjord in June, and in the Baltic as late as November). CHADWICK (1914) gives a somewhat schematic figure of the full-grown larva. Finally, MORTENSEN (1931) gives a beautiful figure of a living larva. The larva is easily recognisable by its broad full arms, which give the whole larva a "fleshy" appearance. The stomach is green, the body otherwise colourless apart from a crimson colour on the tips of the longest arms.

B. Own remarks. The larva is common in the autumn plankton from the Sound. In our samples it is present, taken off Ven, from: $^{17}/_{10}$-36; $^{1}/_{11}$-36; $^{12\text{-}13}/_{8}$-37; $^{21}/_{8}$-37; $^{12}/_{9}$-37; $^{24}/_{9}$-37; $^{10}/_{10}$-37; $^{11}/_{9}$-38; $^{8}/_{7}$-39; $^{13\text{-}14}/_{7}$-39; $^{5}/_{8}$-39, and $^{16\text{-}23}/_{8}$-44, and off Helsingør from: $^{7}/_{10}$-41 (in metamorphosis); $^{17}/_{8}$-42 (54 spms.), and $^{5}/_{9}$-42 (1 spm.). Thus it occurs from the middle of July to September or October. The larva is never present in large numbers (maximum 20—50 larvae per ten samples), and in the autumn samples it is little dominant compared with the large numbers of *Amphiura* larvae.

Psammechinus miliaris (GMELIN). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. The pelagic larva has been identified by MORTENSEN (1898), and has been reared to the young bottom stage by MCBRIDE (1898, 1903), THÉEL (1902), and SHEARER, MORGAN and FUCHS (1913). Finally, MORTENSEN (1924) figures the larva of this species. In stage I the larvae have prolonged body rods, flat, broad, and somewhat branched at the distal end; in stage II the larvae differ from those of *Echinus esculentus* by the absence of posterior epaulettes. Orton observed (1914 a) that ripe specimens of *Psammechinus miliaris* often sit closely together two and two — now and then three or more — and that two-thirds of all "pairs" examined consisted of a male and a female specimen. His conclusion, that a primitive sort of mating takes place, is questioned by Mortensen (1943 p.136), who is of opinion that they crowd under the stones to seek shelter against the light, and recommends observations on crowding specimens also outside the breeding season. The species reaches maturity already in the first year. Breeding takes mainly place in the early summer months, but ripe specimens may be found throughout the greater part of the year, at any rate from early February to late November (Mortensen 1943, p.135—136).

B. Own remarks. This larva is very commonly met with in the plankton, but always in small numbers; it was taken off Ven on the following dates: $^{19\text{-}20}/_{8}$-36; $^{26\text{-}27}/_{9}$-36; $^{17\text{-}19}/_{10}$-36; $^{2}/_{11}$-36; $^{2}/_{5}$-37; $^{12}/_{9}$-37; $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{11}/_{9}$-38; $^{24}/_{9}$-38; $^{25}/_{3}$-39; $^{10}/_{4}$-39; $^{18}/_{8}$-39, and $^{16}/_{9}$-39, and off Helsingor on: $^{14}/_{9}$-41 (older and metamorphosing spms.); $^{17}/_{9}$-41 (one metamorphosing spm.); $^{7}/_{10}$-41; $^{25}/_{10}$-41; $^{2}/_{12}$-41; $^{27}/_{4}$-42 (70 spms.); $^{15}/_{5}$-42 (10 spms.), and $^{5}/_{9}$-42 (8 spms.). Thus this species seems to be present in the plankton from early spring to early December. Larvae in stage I are more common than larvae in stage II, but both stages are found together during the whole larval season, stage II, however, most commonly in the autumn. In 1939 two larvae in stage II were found as early as $^{25}/_{3}$-39 (i. e. earlier in the spring than any other Echinoderm larva in the Sound). This stage is rather densely spotted with carmine, while stage I is quite colourless. In stage II the young bottom stage inside is often provided with suckers, which enable the larva to adhere to a substratum. Young metamorphosed bottom stages were taken in bottle collectors on $^{23}/_{8}$-39; $^{29}/_{8}$-39; $^{2}/_{9}$-39, and $^{21}/_{10}$-39. — An adult female of this species spawned in an aquarium at Ven on $^{10}/_{8}$-36. An adult male from Hellebæk, 35 m depth, spawned ripe sperms in an aquarium on $^{12}/_{9}$-41, and had large, white, swollen testes. Specimens of *Psammechinus miliaris* from the Little Belt were ripe in the first ten days of July, and artificial fertilisation proved very successful (information by Dr. P. L. Kramp).

Echinus esculentus (Linné). Northern part of the Sound, young specimens only, not common.

Reproduction: A. Literature. McBride (1898, 1902, and 1903) and Shearer, Morgan, and Fuchs (1913) have reared this species during the pelagic stage to young bottom forms. Mortensen (1898, p. 97) describes the larval stage II under the name of *Echinopluteus Théelii,* and (1924) figures the body rods in stage I, and a larva in stage II. Stage I is characteristic by having thin, spined body rods, which are bent towards each other at the distal ends. Stage II has epaulettes at the base of the postoral and postero-dorsal arms, and (in contrast to *Psammechinus miliaris*) around the rear part of the body. The young reach maturity already in the first year (Mortensen 1943, p. 35).

B. Own remarks. As mentioned by Mortensen (1924), no distinct characters have been pointed out by which stage II of *Echinus acutus, Echinus esculentus,* and *Strongylocentrotus droebachiensis* can be distinguished with absolute certainty. Two types of such unpigmented larvae in stage II with an epaulette on the rear part of the body are found in our samples. One of them, which seems to be identical with "*Echinopluteus coronatus*" Mortensen (1897 a), and supposed by the same author (1924) to be the larva of *Strongylocentrotus droebachiensis* (cf. this), is present from $^{3}/_{4}$-38 (2 larvae), and from $^{13}/_{8}$-38 (1 larva). The other type, agreeing closely with the drawing of *E. esculentus* "stage II" by MORTENSEN (1924), is present from $^{24}/_{9}$-36 (1 larva) and from $^{9}/_{10}$-37 (1 larva). All stages present of these two types belonged to "stage II", i. e. they were older larvae, while all larvae of regular Echinids in "stage I" (besides *E. acutus*, cf. this) belonged exclusively to *Psammechinus miliaris* (flat, somewhat branched body rods). This seems to show that the larvae of *E. esculentus* and *S. droebachiensis* in the Sound are "drift larvae", and that the population of adults is recruited from the Kattegat.

Echinus acutus LAMARCK. The bottom stage is unknown from the Sound.

Reproduction: A. Literature. The pelagic larva was reared to the young bottom stage by SHEARER, MORGAN, and FUCHS (1913). The body rods in "stage I", which are bent like those of *E. esculentus*, but much more branched, spiny and robust at the distal end, are figured by MORTENSEN (1924). The larva tentatively referred to *E. acutus* by MORTENSEN (1898) according to the same author (1943, p. 49) is probably that of *Psammechinus microtuberculatus*.

B. Own remarks. One larva of this species in "stage I" was taken in plankton off Ven on $^{14}/_{11}$-37. The body rods were branched in precisely the same way as figured by MORTENSEN. The postero-lateral arms, however, were faintly fenestrate at their distal ends — a feature which, according to MORTENSEN (1924), is only found in Spatangid larvae and in the larvae of *Echinocyamus pusillus*. Since the latter species is very characteristic even in the younger stages, I first believed that the larva found was an abnormal Spatangid larva which had lost its posterior rod. A closer examination showed, however, that the way in which the body rods in the *Spatangidae* join the posterior rod differs so greatly from the body rod construction in our larva that it must belong to a regular Echinid, i. e. *Echinus acutus*. The larva was spotted with small carmine pigment grains.

Strongylocentrotus droebachiensis (O. FR. MÜLLER). Northern and middle parts of the Sound, rather common locally.

Reproduction: A. Literature. S. RUNNSTRÖM (1927c) describes the spawning and larval development from Bergen. The breeding season here is January to February, while in Arctic seas the species spawns in the summer. The pelagic development at Bergen (at 4° to 5° C.) takes about $2^1/_2$ months. Several stages up to the full-grown larva are figured. AGASSIZ (1864) was the first to rear the young plutei, while some of his older larvae taken from plankton belong to this species and others to quite different genera (cf. MORTENSEN 1943, p. 210). MORTENSEN (1897a and 1898) describes and figures an older pluteus, *Echinopluteus coronatus* from the Kattegat (April to May), which he later (1924) assumed to be an old larva of *S. droebachiensis* — an assumption which he was able to confirm in 1943 (p. 210). The most characteristic features of this larva are, in "stage I": the long slender body rods, and in "stage II": "epaulets at the base of the main arms, and at the posterior end" (1943, p. 210). A detailed drawing of a full-grown living larva is still a desideratum. The same author mentions (l. c. p. 211) that "at least some specimens breed in summer in Danish seas".

B. Own remarks. During my wintering in East Greenland in 1931—32 I found the larvae of *S. droebachiensis* in the plankton; this species was the only regular Echinid occurring in the fjords there. Unfortunately I had no opportunity to sketch the larva, but on comparing the larvae I then observed with MORTENSEN's figures, I can say that the East Greenlandic larvae of *S. droebachiensis* bear a close habitual resemblance to the *Echinopluteus coronatus*, since they are quite colourless, less broad than the *E. esculentus* larva, and with the arms forming a narrower bundle than in the latter species. — In our main series from the Sound the larvae of this species are remarkably rare. They were collected off Ven on $^{3}/_{4}$-38 (stage II, 2 spms.) and $^{13}/_{8}$-38 (stage II, 1 spm.), and off Helsingør on $^{10}/_{4}$-42 (stage I, 4 spms.). The material is accordingly very sparse and by no means commensurate with the frequency of the adults in the Sound. As mentioned above, these are rather common locally, being especially associated with the epifauna in deeper water, but do not by far reach the frequency of for instance *Psammechinus miliaris*. The larvae in "stage I" found off Helsingør in April agree fairly well with Runnström's and Mortensen's statements, viz. that spawning takes place in winter and spring, and the young larvae seem to originate from parents living in the Sound or the adjacent seas. Out of seven larvae taken in the main series during 4 years, however, three were large larvae just ready to metamorphose. The paucity of these larvae in the Sound may probably be explained by the assumption that the stock of *Strongylocentrotus* in the Sound will spawn eggs and larvae which will generally be carried southwards with the bottom current, where they will be killed by the Baltic water before reaching a stage in which they can be recognised as *Strongylocentrotus* larvae (at 4—5° C. they take 3 days to pass from fertilisation to the gastrula stage, cf. Runnström 1927c). The stock in the Sound is, however, recruited from larvae in the Kattegat, and the old larvae met with just ready to metamorphose are probably the last representatives of a larval crowd from the Kattegat, where the largest number of larvae have already metamorphosed and settled before the arrival of the water mass in the Sound. The main waste in the larval stock must accordingly have taken place in the Kattegat, and nearly all the larvae which reach the Sound will be ready to settle and to grow at once (cf. further pp. 394—396).

Echinocyamus pusillus (O. Fr. Müller). Northern and middle parts of the Sound, common.

Reproduction: A. Literature. In a valuable paper Théel (1892) has described and figured the whole larval development of this species from Kristineberg, where he reared it through the metamorphosis. The breeding season occurs in the summer. The eggs measure 160 μ in diameter, the egg membrane (32 μ thick) not included. The development from fertilisation to metamorphosis takes about 2 months. The young larvae crowd at the surface of the water. Mortensen (1897a, 1898, 1924, and 1931) has likewise figured the larva of this species, which is very characteristic with its frame-shaped body skeleton, and its fenestrate postoral and postero-lateral arms. Mortensen (1897a) records it from the Sound, the Kattegat, and the Limfjord in the period June to September.

B. Own remarks. The larva is common in the Sound plankton, where it was taken off Ven on the following dates: $^{26-27}/_{9}$-36; $^{24-27}/_{7}$-37; $^{12-13}/_{8}$-37; $^{4}/_{9}$-37; $^{12}/_{9}$-37; $^{24}/_{9}$-37; $^{9}/_{10}$-37; $^{5}/_{12}$-37; $^{26}/_{8}$-38; $^{24}/_{9}$-38; $^{15}/_{7}$-39; $^{18}/_{8}$-39, and $^{19}/_{8}$-44, and off Helsingør on: $^{14}/_{9}$-41 (in metamorphosis); $^{7}/_{10}$-41 (3 young metamorphosed spms.); $^{25}/_{10}$-41 (1 late spm.); $^{25}/_{7}$-42 (3 spms.); $^{17}/_{8}$-42 (18 spms., one crawling), and $^{5}/_{9}$-42 (4 spms.). Thus, larvae occur in the period July to December, attaining their maximum in September-October. In the main season 5 to 20 larvae were taken in 10 samples. Young as well as older larvae occur, and larvae with a young bottom stage formed inside were met with as early as $^{17-18}/_{8}$ while the larva from $^{5}/_{12}$ had not yet formed a bottom stage. Young metamorphosed bottom stages were taken in bottle-collectors on $^{23}/_{8}$-39.

Spatangus purpureus O. Fr. Müller. Taken off Kullen, not in the Sound proper.

Reproduction: A. Literature. Krohn (1853, 1854) was the first to rear the larvae at Messina (artificial fertilisation), and he described and figured the young larva (metamorphosis not observed). His description has been republished by Mortensen (1897 a, 1898) who, however, was personally able to rear the larva at Plymouth (1913) to the full pelagic stage, which he describes and figures. In June to July the larvae took 3 weeks to reach their full pelagic size with the first signs of metamorphosis. The postero-lateral processes are long and slender (like those of *Echinocardium cordatum*, but unlike those of *Brissopsis lyrifera*), the posterior rod is exceptionally long, and the same applies to the postoral, and the postero-dorsal processes. Mortensen (1913, p. 15) is of opinion that the larvae caught in the plankton and described by Krohn (see above) do not belong to *S. purpureus* but to another Mediterranean *Spatangoid*.

B. Own remarks. A young larva with an extremely long posterior rod was found in our samples taken off Ven on $^{9}/_{10}$-37. In other samples, also, posterior rods longer than those described for the *Echinocardium* larva have been found, but they all proved to be derived from abnormally developing larvae of *Echinocardium*. In such larvae, however, the posterior rod will never attain the enormous length characteristic of the *Spatangus* larva. This larva is the only one found in the Sound.

Echinocardium cordatum (Pennant). Northern and middle parts of the Sound, very common.

Reproduction: A. Literature. Moore (1936) gives interesting data on the breeding near the Isle of Man: maximum breeding in June-July-August. The animals reach maturity in their second year. Fifty per cent of the adult males were ripe in March, and all of them in April, while the females commence ripening in April, and all of them are ripe in June. — Mortensen (1897 a, 1898) was the first to describe and figure the larva (from Danish waters). Later on McBride (1914 and 1918) has reared the larva (artificial fertilisation) to the young bottom stage. The egg is "not a sphere but an ellipsoid", the size of the egg is not given. The development is rapid, full-grown larvae occur 14—16 days after fertilisation, and the metamorphosis is completed 24—30 days after fertilisation. Mortensen (1931) gives a beautiful figure of the full-grown larva from Kristineberg. Characteristics are: the rather long postero-lateral processes (in contrast to those of *Brissopsis lyrifera*), the moderately long posterior rod, the yellowish stomach, and the bright crimson pigment at the tips of all the rods and arms. The same author (1897 a) reports this larva from the Limfjord and the Kattegat from June to September.

B. Own remarks. The larva, which is common in the Sound, was found in our samples from the following dates, collected off Ven: August 1936; $^{26\text{-}27}/_{9}$-36; $^{17}/_{10}$-36; $^{23}/_{7}$-37; $^{9}/_{8}$-37; $^{12\text{-}13}/_{8}$-37; $^{21}/_{8}$-37; $^{17}/_{7}$-38; $^{11}/_{9}$-38; $^{4}/_{6}$-39; $^{17}/_{6}$-39; $^{3}/_{7}$-39; $^{13\text{-}14}/_{7}$-39; $^{5}/_{8}$-39; $^{18}/_{8}$-39, and $^{16\text{-}19}/_{8}$-44, and off Helsingør on: $^{8}/_{7}$-41; $^{11}/_{7}$-41; $^{17}/_{9}$-41; $^{7}/_{10}$-41; $^{4}/_{6}$-42 (young spms.); $^{6}/_{7}$-42 (young spms.); $^{18}/_{7}$-42 (young spms.); $^{25}/_{7}$-42; $^{17}/_{8}$-42 (young as well as metamorphosing spms.), and $^{5}/_{9}$-42 (young as well as metamorphosing spms.). Thus larvae occur regularly in the months June-October with their maximum occurrence in August-September. In June-July only very young larvae are met with, and normally only in rather small numbers. The August-September maximum, however, consists mainly of older larvae, and larvae with a young bottom stage formed inside (up to 90 larvae per 10 samples). The total number of larvae from the Sound shows very clearly that older larvae and larvae with a bottom stage inside are much commoner than young larvae — a phenomenon which no doubt indicates that the majority of *Echinocardium* larvae in the Sound originate from Kattegat-parents and are carried into the Sound with the south-flowing bottom current. This is easily understood if we consult the paper of Brattström (1941), which shows that a rather high percentage (about 50 per cent, in some localities up to 90 per cent) of the *Echinocardium* population in the Sound is infected by a parasitic *Ascothoracid*, which sterilises the adult animals and thus prevents them from reproducing. The *Echinocardium* stock in the Sound depends, therefore, to an even greater extent than the populations of other Echinoderms in the Sound on "drift larvae", which will normally occur in a sufficiently large number to maintain the stock. Larvae nearly ready to metamorphose are able to crawl on the bottom by means of the suckers of the young bottom stage formed inside. Larvae with such bottom stages formed inside were found as early as $^{24}/_{7}$-37. Young metamorphosed bottom stages were taken in bottle-collectors off Ven on $^{23}/_{8}$-39; $^{29}/_{9}$-39; $^{2}/_{9}$-39, and $^{21}/_{10}$-39.

Echinocardium flavescens (O. Fr. Müller). Northern part of the Sound, very rare.

Reproduction: A. Literature. Chadwick (1914) describes and figures a larva from Port Erin plankton (February to April) which he thinks should be referred to this species. Mortensen (1920 a), however, discusses the finding of Chadwick and arrives at the conclusion that "the reference of the larva to *Echinocardium flavescens* in any case is uncertain", and "it cannot . . . be decided whether Chadwick's larvae belong to *Brissopsis* or perhaps to *Echinocardium flavescens*". Further, Mortensen (l. c.) has examined a large number of adult specimens of this species near Kristineberg, and found that the breeding season had ceased already at the end of July, and that judging from the small egg size the larvae must be pelagic. Thus the larva itself is still unknown.

B. Own remarks. The plankton from the Sound contained no Spatangid larvae which could be distinguished from those of *Echinocardium cordatum*, *Brissopsis lyrifera*, and *Spatangus purpureus*. Possibly the larva in question is very similar to that of *E. cordatum*, with which it may accordingly have been confused. Since, however, *E. flavescens* breeds early in the summer at Kristineberg, and since Spatangid larvae in the Sound are not very predominant in the plankton until August, the larva of *E. flavescens* — if at all present — hardly plays any great part in the Sound plankton.

Brissopsis lyrifera (Forbes). Northern part of the Sound, not very common.

Reproduction: A. Literature. The larva is described and figured by Mortensen (1920 a) from plankton near Kristineberg, where it occurs in September. Characteristic features are that the postero-lateral arms are reduced to "a pair of small ear-shaped lobes, not supported by a skeletal rod", and that "the postoral, postero-dorsal and posterior rods are fenestrated only in the outer part". According to verbal information from Dr. Mortensen some doubt still prevails as to whether the larva figured by him is actually the oldest larval stage, and the possibility still remains that the postero-lateral arms are more distinct in a later stage than in the stage figured.

B. Own remarks. A large male taken between Viken and Ellekilde, 35 m depth, on $^{9}/_{7}$-42 spawned large clouds of white sperms when fixed in formalin. In our samples from the Sound larvae were collected on the following dates, off Ven: $^{1}/_{11}$-36; $^{14}/_{11}$-36; $^{12}/_{9}$-37; $^{25}/_{9}$-37; $^{9}/_{10}$-37; $^{23}/_{10}$-37; $^{14}/_{11}$-37; $^{18}/_{12}$-37; $^{6}/_{1}$-38; $^{26}/_{8}$-38; $^{24}/_{9}$-38, and $^{16}/_{9}$-39, and off Helsingør on: $^{25}/_{10}$-41 (several young, a few metamorphosing spms.), and $^{11}/_{11}$-41 (young spms.). Thus larvae occur from late August to early in January, with a maximum in October-November. Young larvae were found as late as December, but — as in *Echinocardium cordatum* — by far the largest number of the larvae found were in the oldest stages and must be assumed to originate from the Kattegat, where the adults are much more frequent than in the Sound. Larvae with a bottom stage formed inside were met with as early as September, and these stages showed that the lateral arms will not appear even in the latest larval stages. The larvae of this species are less common (normally 10–20, maximum about 80 larvae, per ten samples) in the Sound than those of *Echinocardium cordatum*.

Cucumaria elongata Düben and Koren. Northern and middle parts of the Sound, rather common in deep water.

Reproduction: A. Literature. The reproduction is unknown, but it has been described for the related northern species *Cucumaria frondosa* (J. and S. Runnström 1919), for *C. echinata* (Ohshima 1918, 1921), and *C. normani* and *C. saxicola* (both Newth 1916). These species have free-swimming, slipper- or barrel-shaped brick-coloured larvae (no *Auricularia* stage). They move through the water rotating round their own axis by the aid of fine cilia, they are intransparent and yolky and feed on this yolk until metamorphosis, thus taking no nourishment from the plankton.

B. Own remarks. Seven foreign species of *Cucumaria* are known to have brood-protection, while all other species examined have larvae of the type described above. Accordingly *C. elongata*, not having brood protection, must be supposed to reproduce by similar brick-coloured, slipper-shaped larvae as those described above. Larvae of this type were actually found in our samples on several occasions, but when reared through metamorphosis they proved to belong to *Psolus phantapus* (which see), not to *C. elongata*, the larvae of which are thus still unknown.

During a stay in the Gullmarfjord (Bohuslän, Swedish W. coast) in August 1945, I observed in the plankton a barrel-shaped larva, which had precisely the same shape, and was in the same stage of development as the *Psolus* larva reproduced in fig. 192 B in this paper. The length of the Gullmarfjord larva (500 μ) was, however, less than half the length of the *Psolus* larva (1050 μ), and the colour was greyish-green, not brick-coloured as in *Psolus*. It seems therefore most reasonable to refer this larva to a species of *Cucumaria*, especially as *Cucumaria lactea* and *C. hyndmanni* are very common in the Gullmarfjord.

Thyonidium pellucidum Düben and Koren. Common in the northern and middle parts of the Sound.

Reproduction: A. Literature. Unknown.

B. Own remarks. As mentioned above nothing is stated in the literature concerning the reproduction of this species, but since the eggs are large and yolky, and larvae of *Auricularia* are so far unknown within the *Dendrochirota*, the species must be supposed either to have similar slipper- or barrel-shaped, brick-coloured larvae to those known from *Cucumaria* and *Psolus* or to reproduce in an entirely unpelagic way. As, however, *T. pellucidum* is extremely common round our fixed plankton stations near Ven and along the whole W. coast of Ven, it can be taken for granted that the larvae, if pelagic, would have appeared in our regular plankton samples. However, no such larvae were present, and accordingly it seems most likely that this species has a non-pelagic development. As the adult specimens kept in the collections of the Copenhagen museum have all of them been collected and fixed in the summer, it is quite possible that the species breeds in winter and has brood-protection or is viviparous. — Detritus samples taken off Ven on $^{10}/_{8}$-36 contained several young specimens about 5 mm long.

Phyllophorus communis Forbes. Northern and middle parts of the Sound, rare.

Reproduction: Not described in the literature and unknown from the Sound.

Psolus phantapus (Strussenf.). Northern and middle parts of the Sound, rather common.

Reproduction: A. Literature. Spawning specimens have been observed in aquaria at Bergen in February and March. The eggs float in the water, are pink with a yellowish tinge, ellipsoid, largest diameter 590 μ (Nordgaard 1912). Mortensen (1897 a) figures and describes larvae

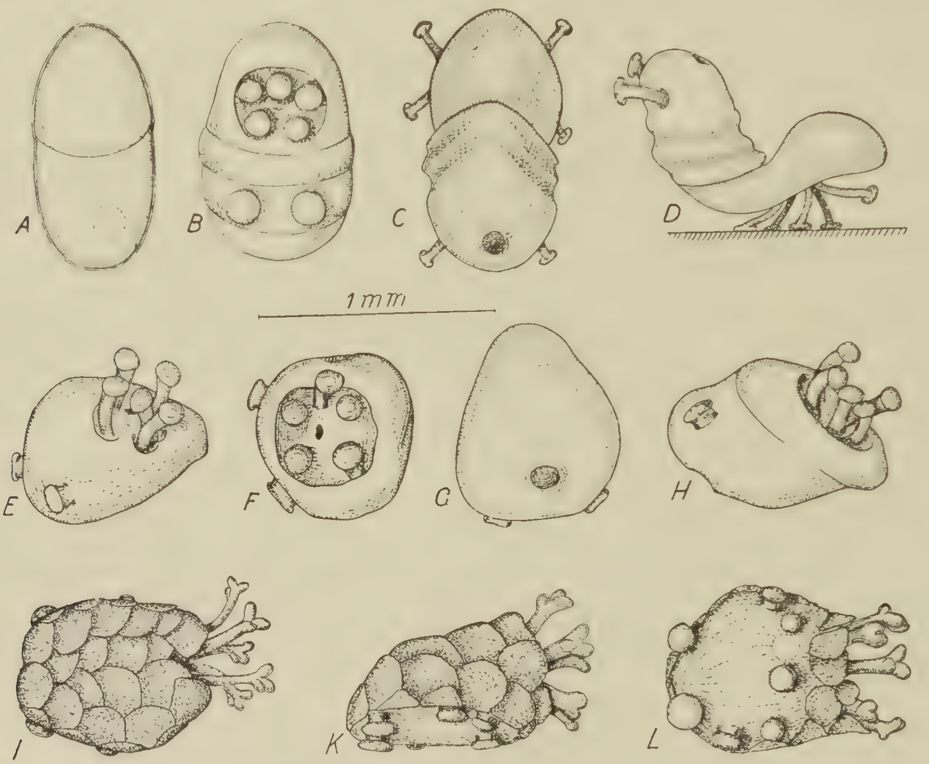


Fig. 192 A-L. *Psolus phantapus* (Strussenf.). — Larval development. — *A*. Young larva, and *B*. Older larva from plankton off Ven, taken on $^{5}/_{6}$-1939 (drawn from life on $^{8}/_{6}$-1939). — *C*. Larva in the "floating-crawling stage". Four tentacles, two suckors, and the anal opening are seen. — *D*. The same larva seen from the right side attached by the tentacles to a substratum (both from plankton off Ven, taken on $^{17}/_{6}$-1939). — *E* to *H*. The larva fig. B after having been kept in an aquarium for four days at 20° C. The larva was healthy and active, shorter and broader than the planktonic stage, with five very mobile and sticky tentacles. Two suckors and anal-opening distinct. Although normally adhering, the larva was still able to swim rather rapidly forwards as well as backwards without rotating on its longitudinal axis. E and H from the right side, F from the oral side, G from the anal side with tentacles and mouth attached to the substratum (drawn from life on $^{10}/_{6}$-1939.) — *I* to *L*. Youngest metamorphosed bottom stage known. Attached to shell of *Balanus*, taken off Ven, depth 10 to 16 m, on $^{11}/_{7}$-1939 (drawn from life on $^{14}/_{7}$-1939). I seen from the dorsal side, K from the right side, and L from the ventral side.

which he refers with some doubt to this species. They are of a faint reddish colour, opaque, 1 mm long, and occur rather frequently in plankton from southern Kattegat and the Great Belt in April-May. J. and S. Runnström (1919) describe the development of this larva from Bergen. They figure the first stages of development and the young gastrulae, and state that the occurrence of the larvae is limited to March-April. The eggs of *Psolus* are of a red colour like those of *Cucumaria frondosa*, but more faintly coloured. The last-mentioned paper, however, mentions the great habitual similarity as well as the similar development within the different barrel-shaped larvae of Holothurians. Thus the authors in question are unable to decide whether the fixed Holothurian larvae from Greenland belong to *Cucumaria frondosa* or to *Psolus phantapus* — two types the embryology of which they have studied in detail!

B. Own remarks. The literature cited above mentions the great difficulties that are connected with the identification of the larval type described — a type, which may be found in the *Cucumaria* species as well as in the *Psolus* species in the Danish waters. Larvae of this type were collected in the Sound off Ven on the following dates: $^{23}/_{7}$-37 (1 spm.); $^{24}/_{7}$-37 (2 spms.); $^{27}/_{7}$-37 (1 spm., pump water from $16^{1}/_{2}$ m depth); $^{5}/_{6}$-39 (2 spms.), and $^{17}/_{6}$-39 (3 spms. in the main series, and 9 spms. in the supplemental series); $^{3}/_{7}$-39 (1 larva in the crawling stage), and off Helsingor on: $^{10}/_{4}$-42 (2 young spms.); $^{27}/_{4}$-42 (5 young larvae). Thus the larvae occur in the months April-July, i. e. later than recorded from Bergen (March-April), and from the Kattegat-Belt-Sea (April to May). In only 3 of these 26 larvae (from $^{5}/_{6}$-39 and $^{10}/_{4}$-42) the 5 tentacles had not developed. All the other 23 larvae found were able to swim by means of a very fine ciliated surface, and to crawl by the aid of their 5 tentacles. Specimens placed in aquaria on $^{5}/_{6}$-39 had commenced metamorphosis on $^{10}/_{6}$, and on $^{14\text{-}15}/_{6}$ they were found to develop calcareous plates on the surface, but they died on $^{16}/_{6}$. Similar larvae placed in aquaria on $^{17}/_{6}$-39 showed a quite identical development, and died in a stage in which the calcareous plates showed that they could not be the larva of *Thyonidium pellucium* (to which species we had first referred them), but pointed to *Psolus phantapus*. Finally, on $^{11}/_{7}$-39 a just metamorphosed bottom stage of *Psolus* (attached to a shell of *Balanus* taken just inside our fixed plankton station, at a depth of 10—16 m) confirmed our conjecture. On $^{11}/_{7}$-41 large numbers of young bottom stages were found on *Cyprina* shells, slags, and *Furcellaria* off Hellebæk, in the *Modiola* epifauna at a depth of 35 m. The young had just settled, and were easily discernable owing to their orange colour. They were present in all stages, from such in which the calcareous plates had just formed to stages somewhat older than the oldest young figured from Ven. The time for settling agrees well with the time for larval occurrence found in our main series. The growth of the young bottom stages seems to be rather slow. Thus a dredge haul taken at the same depth and in the same locality on $^{12}/_{9}$-41 contained large numbers of young only 2—3 mm long — all originating from the spawning in the same year. The larvae secured showed that they do not feed until they have metamorphosed, and thus they take no nourishment from the plankton, i. e. they are lecithotrophic. — The whole development from the youngest pelagic stage to the metamarphosed bottom stage is shown in fig. 192 A-L.

Leptosynapta inhærens (O. Fr. Müller). Middle part of the Sound, not common, probably often overlooked.

Reproduction: A. Literature. S. Runnström (1924 and 1927 b) has observed the spawning and describes and figures the larva of this species from Bergen. Breeding season at Bergen August to September. Eggs small (200 μ in diameter); free-swimming gastrulae about 24 hours after fertilisation. Larvae three days old are barrel-shaped, with four distinct transverse bands of cilia. Thus no *Auricularia* stage is developed. This is a most remarkable fact, for the small eggs with a small content of yolk pointed to a typical *Auricularia* (Mortensen 1924). In the aquaria the larvae swam near the bottom; they were looked for in the plankton, but in vain; their free-swimming life is short.

B. Own remarks. No larvae of this type were found in our samples from the Sound. Quite possibly, however, the larvae were confused with young Trochophores of Polychaetes during the first year of our investigation.

General Discussion of the Echinodermata.

According to Brattström (1941) the bottom stages of 30 species of Echinoderms are known from the Sound. To these may be added two species of which only the larval stages are known from the Sound, viz. *Echinus acutus* and *Spatangus purpureus*; only one larva of each species has been found.

For 26 of these 32 species the larval development is known and can be classified as follows (for species marked with an asterisk new data concerning their reproduction or larval occurrence in the Sound are given in the special part of this paper):

A. Viviparous species: 1 = 3.9 per cent., viz. **Amphipholis squamata.*

B. Species with brood protection: 2 = 7.7 per cent., viz. *Henricia sanguinolenta,* and *Asterias mülleri.* The brood protection is external; the eggs and embryos develop in the space formed between the substratum, the arms, and the disc. The eggs are large and yolky, and the embryos feed exclusively on their own contents of yolk until metamorphosis. The eggs and embryos of both species will develop in precisely the same way when removed from the mother animal, and eggs and embryos of *Henricia sanguinolenta* may (at Millport) under natural conditions float in the water without any brood protection, and develop well. From an ecological point of view such embryos may just as well be referred to the following type, viz.:

C. Species with pelagic, lecithotrophic larvae (cf. pp. 436—438): 4 = 15.4 per cent., viz. **Solaster endeca, Solaster papposus, *Psolus phantapus,* and *Leptosynapta inhærens.* Such larvae, though pelagic, will take no nourishment from the plankton, but will develop until metamorphosis exclusively on their own contents of yolk. Their planktonic stage is only of value for the distribution of the species, and is of no importance as a feeding stage. The other dendrochirote Holothurians occurring in Danish waters the development of which is still unknown, will probably also prove to belong to this larval type.

D. Species with pelagic, planktotrophic larvae (cf. pp. 432—435): 19 = 73.1 per cent., viz. **Astropecten irregularis, Luidia sarsi, *Asterias rubens, *Ophiothrix fragilis, *Ophiocomina nigra, Ophiopholis aculeata, *Amphiura filiformis, Ophiura texturata, Ophiura sarsi, *Ophiura robusta, *Ophiura albida, *Psammechinus miliaris, *Echinus esculentus, *Echinus acutus, *Strongylocentrotus droebachiensis, *Echinocyamus pusillus, *Spatangus purpureus, *Echinocardium cordatum,* and **Brissopsis lyrifera.*

Accordingly the embryos, the larval stages, or the young metamorphosing stages of 18 of these 26 species in which the mode of development is known were observed during our investigations in the Sound.

Twenty-three out of these 26 species, i. e. 88—89 per cent, have pelagic larvae.—The adults of several Echinoderms are fairly common in the Sound. Judging from 300 bottom samples taken all over the northern and middle parts of the Sound (Petersen 1911, table VI, No. III—VIII) the adult Echinoderms with pelagic larvae represent 30 per cent. of all the invertebrate specimens with a pelagic development on the level bottom, and a rough calculation would seem to show that they represent about 20—25 per cent of all the pelagically developing invertebrate specimens in the Sound, if also the epifauna animals are included (cf. this paper p. 393). It might therefore be anticipated that they play a very important part within the stock of pelagic larvae in the Sound. However, this is not the case. Of the total number of larval bottom invertebrates from our main series the Echinoderm larvae represent only 0.8 per cent. (off Ven, 45 main series), and 3.2 per cent. (off Helsingør, 20 main series), or 1.9 per cent of the total number of larvae of all the main series from Ven and Helsingør (cf. further pp. 394—396). It should likewise be emphasised that nearly all Echinoderm larvae found in the Sound occur in the Kattegat water, which — unlike several other invertebrate larvae — they only very seldom leave to ascend through the spring layer to the brackish surface water (cf. p. 390).

If these data are viewed in connection with the fact that the predominant Echinoderm larvae in the Sound seem to be fairly common in the older stages just ready to metamorphose, while young stages are uncommon or even rare, it seems justifiable to conclude that most of these larvae originate from the Kattegat and have been drifted into the Sound with the south-moving bottom current. This seems for instance to be the case with three of the commonest larval types, viz. *Amphiura filiformis* (p. 349), *Echinocardium cordatum* (p. 357), and *Brissopsis lyrifera* (p. 358) (cf. also *Strongylocentrotus droebachiensis* p. 355). The young eggs and larvae spawned in the Sound will usually be carried southwards with the bottom current, and within the area Taarbæk-Barsebäck-Limhamn-Amager they will be forced into the Baltic water and perish there. It is a matter of fact that Echinoderm larvae are much more sensitive to changes in the salinity and temperature than for instance larvae of Gastropods, Lamellibranchs, and most Polychaetes. In our main series the Echinoderm larvae were always the first to die, and they were often in full dissolution when the other groups of invertebrate larvae were still vigorous and healthy. Our pump series (cf. pp. 381—392) showed that the lower stratum of the north-flowing surface water in the summer and autumn contains a layer of dead Echinoderm larvae in various stages of dissolution, but no similar layer of dead Gastropod- or Lamellibranch-larvae was found (cf. pp. 395—396).

The conditions of the Echinoderm larvae in the Sound seem, then, to be as follows: eggs and larvae originating from parents in the Sound and the neighbouring areas of south-eastern Kattegat will be killed by brackish water before reaching a stage in which they are recognisable as Echinoderm larvae during a rapid sorting of a planktonic main series. The stock on the bottom is recruited from larvae living in the middle and southeastern parts of the Kattegat, and the older larvae so commonly met with in the Sound must be regarded as laggards of the large larval swarms occurring in the Kattegat. Most of the larvae in these swarms seem to have metamorphosed and left the plankton before the water masses reach the Sound, but these few laggards — often with the young bottom stage formed inside, and just ready to settle without any large "waste" — have proved to be present in sufficiently large numbers to renew the stock on the bottom.

Another point which has probably some influence on the low percentage of Echinoderm larvae in the Sound is the relatively small number of eggs spawned per female per season by those species of Echinoderms which are predominant in the Sound and in southeastern Kattegat. It is a well known fact that certain Echinoderms are able to spawn immense numbers of eggs during a single spawning. Such large spawnings are especially known from Asterids and regular Echinids. Of the Asterids may be mentioned: *Asterias rubens* (2 million eggs per female in a single spawning), *Luidia ciliaris* (200 million eggs per female per season), and of the regular Echinids: *Diadema setosum* (millions of eggs per specimen, see further this paper pp. 440—441). But in the Sound and southeastern Kattegat precisely these two groups play a much smaller part on the bottom than in other European seas with a higher salinity at the surface. The dominating Echinoderms in the Sound, especially the Ophiurans, seem, however, to produce surprisingly few eggs per female. Thus Dr. Mortensen has kindly informed me that in *Amphiura filiformis* the number of eggs spawned per female per season may be estimated at about 5,000 only (all spawned in a single spawning per year), and no doubt the other Ophiurids in the Sound, *Ophiura albida* and *Ophiura robusta*, spawn about the same number of eggs. Compared with the much larger number of eggs spawned by nearly all the Lamellibranchs, and several Polychaetes, Gastropods, and Nemertines with pelagic larvae in the Sound, it seems evident that this low "spawning intensity" of the dominant Echinoderms in our area will likewise contribute to reduce the percentage of Echinoderm larvae in the plankton. The percentage of Echinoderm larvae actually found in the Sound plankton is, however, so low that it can only to a small extent be accounted for by the small number of eggs shed per female.

Fig. 193 p. 375, and fig. 194 p. 377 show the occurrence of Echinoderm larvae in our main series taken off Ven and off Helsingor respectively. The table on p. 372 is a supplement to the figures from Ven, and comprises the months from August 1936 to August 1937, from which the number of larvae collected has only been estimated but not exactly counted. The series from Ven shows a distinct maximum in the months August to November, consisting of several species of larvae. From the end of December to the end of March or the beginning of April all the Echinoderm larvae are totally absent from the plankton, then, in April to June, a small spring maximum sets in, consisting mainly of the larvae of *Ophiura robusta*. Off Helsingor the same two maxima are found, but here the spring maximum (up to 1600 larvae per main series) is predominant, though it mainly consists of large numbers of *Ophiura robusta* larvae and a few *Psammechinus* larvae. Here, also, the largest number of larval species is found in the late summer and autumn.

Starting with the spring maximum, from the end of April to June, with larvae of *Ophiura robusta, Psammechinus miliaris, Strongylocentrotus droebachiensis,* and *Psolus phantapus*, we meet, in June, the young *Asterias rubens* larvae — the only Echinoderm larvae belonging to the "summer spawning" ("the Baltic spawning", cf. pp. 402—405). Then, after a nearly total absence of Echinoderm larvae in late June and early July, the "autumn spawning" sets in early in August with its forerunners: *Ophiura albida, Amphiura filiformis,* and *Echinocardium cordatum*, supplemented late in August and early in September by the larvae of *Ophiothrix fragilis, Ophiocomina nigra, Echinocyamus pusillus,* and *Brissopsis lyrifera*, until they all decrease rapidly in number towards the end of November and the beginning of December, when the plankton will be entirely free from Echinoderm larvae until the spring maximum sets in.

The surprising absence of the normal autumn maximum of Echinoderm larvae in the Sound in 1938, and the reasons why this maximum failed to appear, are discussed in detail on pp. 380—381.

The total number of Echinoderm larvae (3434 larvae) examined in our main series during the three years in which exact counts were made, viz. from Ven 1148 (in 45 main series), and from Helsingør 2286 (in 20 main series), are distributed over the systematic groups as follows:

	Off Ven	Off Helsingør	Total
Larvae of Asterids	6.6 %	2.7 %	5 %
— - Ophiurans	77.0 %	86.8 %	84 %
— - Echinids	15.9 %	10.2 %	11 %
— - Holothurians	0.5 %	0.3 %	0 %
	100.0 %	100.0 %	100 %

The larvae of *Asterias rubens* represent 4.75 per cent of the 5 per cent of Asterid larvae. Of the 84 per cent of Ophiurid larvae, those of *Ophiura robusta* represent 56 per cent, those of *Amphiura filiformis* 26 per cent, and those of *Ophiura albida* 2 per cent only, while the larvae of *Ophiothrix fragilis* and *Ophiocomina nigra* are of no quantative importance at all. The 11 per cent which falls upon the Echinid larva may be divided into more narrow systematic groups, the regular Echinids representing 2 per cent, the *Echinocyamus* larvae likewise 2 per cent., while the remaining 7 per cent fall upon the irregular Echinids. Of the regular Echinids the larvae of *Psammechinus miliaris* are completely dominant, representing nearly all the 2 per cent found for the whole group. The seven per cent which fall upon the irregular Echinids are distributed with 4.5 per cent upon *Echinocardium* larvae, and 2.5 per cent upon *Brissopsis* larvae.

To sum up: The Ophiurid larvae dominate entirely among the Echinoderm larvae in the Sound. The larvae of *Ophiura robusta*, and *Amphiura filiformis* alone constitute no less than 82 per cent of all the Echinoderm larvae known from the area in question. Next come the larvae of *Asterias rubens*, and *Echinocardium cordatum*, constituting 4.75 and 4.5 per cent respectively of the total stock of Echinoderm larvae, followed by *Ophiura albida, Brissopsis lyrifera*, and *Psammechinus miliaris* each with 2.5 to 2 per cent.

As has often been observed for other groups of marine animals also, the number of the individual larval species is not directly proportional to the number of adult animals of the same species found in the Sound. Thus, it might be expected that *Ophiura albida* would have a greater number of larvae than any other species of Echinoderm within the Sound. On the basis of about 850 dredge hauls from 105 stations in the Sound BRATTSTRÖM (1941) states that bottom stages of *Ophiura albida* were present at 74 of these stations, and mentions *Ophiura albida* as a type animal in the Sound (p. 269). The same author writes (p. 186) that *Ophiura albida*, according to an estimate based upon the dredge hauls mentioned above, is not only the most evenly distributed and most frequently found Echinoderm in the Sound, but one of the commonest of all the invertebrates within the area. "*O. albida* scheint der Fauna des Öresundes das Gepräge zu geben". On this basis it almost seems grotesque that the larvae of this species represent only 2.5 per cent of all the Echinoderm larvae in the Sound, and only 0.05 per cent of all the pelagic larvae of invertebrates within the area. This phenomenon, also, may probably be explained by the large sensitiveness of the larvae to changes in the hydrographical conditions, and by the invasion of older larvae from the Kattegat.

Among the Echinoderms in the Sound it seems rather easy to distinguish between the members of the epifauna and those belonging to the infauna, and accordingly it is possible to examine the relative frequency of larvae belonging to these two elements within the plankton of the Sound. As "epifauna larvae" I regard: *Asterias rubens, Ophiothrix, Ophiocomina,* all regular Echinids, *Echinocyamus*, and *Psolus*, while the "infauna larvae" comprise: *Astropecten, Amphiura, Ophiura robusta, O. albida, Spatangus, Echinocardium*, and *Brissopsis*. The distribution of the larvae is as follows:

Ven plankton		Helsingør plankton		Average for both stations	
Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna
1223 larvae	205 larvae	4438 larvae	311 larvae	5661 larvae	516 larvae
= 85.5 %	= 14.5 %	= 93.0 %	= 7.0 %	= 92 %	= 8 %

It will be seen that the "infauna larvae" show a striking dominance in the plankton, as was also to be expected judging from the frequency of the adults. The reasons of this very low frequency of the "epifauna larvae" must partially be sought outside the Sound, i. e. in the southeastern and middle parts of the Kattegat, where the Baltic current is still so predominant at the surface that no or only few Echinoderms are able to thrive in shallow water, where the conditions for larger epifaunas (stone reefs, moles) are much more favourable than in deeper water where level muddy (or sandy) areas prevail. These conditions have for instance expelled *Asterias rubens* from the tidal zone in the northern part of the Sound and in southeastern Kattegat; in localities where it inhabits shallow water (i. e. the Limfjord and northeastern Kattegat) precisely this epifaunal species produces huge swarms of larvae, which dominate entirely in the plankton. In the Sound and in southeastern Kattegat, however, *Asterias rubens* is less frequent, being restricted to somewhat deeper water. — A striking contrast to the Echinoderm larvae in this respect is shown by the Prosobranch larvae in the Sound, among which the "epifauna element" is largely predominant. This is especially due to the larvae of *Littorina littorea* — a species, which in the adult stage is able to survive in the tidal zone in Baltic water, and here occurs in such large numbers that its larvae are able to dominate in the plankton.

All the northern Echinoderms with pelagic larvae spawn their eggs freely in the water. The males are normally the first to spawn, and on surrounding a mature female, the active sperms will induce spawning in this (cf. pp. 443—446). It would seem, therefore, that the "waste" of eggs during failing fertilisation is much smaller than previously supposed, as the eggs are spawned directly into a swarm of active sperms. In their mode of spawning the Echinoderms agree closely with the Lamellibranchs, while some Polychaetes and nearly all Gastropods have a copulation or a pseudocopulation which allows of fertilisation of the eggs in the mother animal or in an egg jelly, that is to say, the sperms and eggs are not in direct contact with the water before the fertilisation takes place. While the eggs and larvae of Echinoderms and Lamellibranchs normally spend their whole life from fertilisation to metamorphosis in the free water masses, several Polychaetes and nearly all Gastropods pass their early development in an egg capsule or an egg jelly. It seems, however, that the free larval life following upon the hatching from these capsules or jellies lasts just as long as the whole pelagic development of the Echinoderm and Lamellibranch larvae.

The duration of the pelagic larval life is discussed in detail on pp. 451—457. From this discussion it would seem that those Echinoderm larvae from northern seas which are reared in nature or under laboratory conditions resembling the natural conditions, will take about 3—4 weeks from fertilisation to metamorphosis when spawned in the warm season (examples are: *Asterias rubens* (4 weeks), *Spatangus purpureus* (3 weeks), *Ophiothrix fragilis* (3—4 weeks), and *Echinocardium cordatum* (3—4 weeks), cf. p. 453). This seems to be in good agreement with the time taken by other pelagic larvae of invertebrates in the same season.

It has been mentioned above that Echinoderm larvae seem to be much more sensitive to changes in the salinity and temperature than most other pelagic invertebrate larvae. On another point, however, the Echinoderm larvae seem to possess an advantage over other larval invertebrates; thus the latter serve in large numbers as food for other animals (cf. pp. 468—471), but this does not seem to be the case with the Echinoderm larvae. Most of their competitors in the plankton seem to avoid them, probably owing to their bristled larval arms. Only Decapod larvae (e. g. of *Porcellana, Galathea, Gebia, Axius* and *Pandalus*) are known to feed regularly on larval Echinoderms.

Summary of the Discussion.

Thirty-two species of Echinoderms are known from the Sound in the form of adults or larvae or both. The larval development is known for 26 of them: 1 is viviparous, 2 have brood protection, 4 have lecithotrophic pelagic larvae, and 19 have planktotrophic pelagic larvae. Thus 23 species, or 88—89 per cent., have pelagic larvae. In the bottom stage the Echinoderms constitute about 30 per cent. of all the invertebrate specimens with pelagic larvae in the infauna, and about 20—25 per cent. if the epifauna is also included, while the larvae represent 1.9 per cent. only of all the invertebrate larvae in the Sound plankton. Larval Echinoderms are much more sensitive to hydrographical changes than are other larval invertebrates. Nearly all the Echinoderm larvae occurring in the Sound live in the Kattegat layer (high salinity); those spawned in the Sound proper are carried southwards, where they will meet with brackish water, and will leave the Sound as a layer of young, dead larvae, which drift northwards in the lower part of the Baltic water layer. The dominance of older larvae in the plankton seems to show that these larvae originate from the Kattegat. Though few in number, these larvae — just ready to metamorphose and settle — are sufficiently numerous to maintain the population of adults in the Sound. Also the small number of eggs produced by each female of the dominating Echinoderms in the Sound and S.E. Kattegat may contribute to explain the low percentage of larvae in the plankton. A spring maximum with *Ophiura robusta* larvae, a summer spawning with *Asterias* larvae, and an autumn maximum with most other Echinoderm larvae is followed by a season — from the end of December to the end of March — which is entirely free from larvae. The Ophiurids constitute 84, the Asterids 5, and the Echinids 11 per cent of all the Echinoderm larvae in the Sound plankton, with *Ophiura robusta* and *Amphiura filiformis* as dominants. Larvae belonging to "infauna parents" comprise about 90 per cent of all the Echinoderm larvae in our main series. In the warm season northern Echinoderm larvae will take 3—4 weeks to pass from fertilisation to metamorphosis. This time is exclusively spent in the plankton. The larvae are of rather little importance as food for other animals.

V. General Remarks on the Reproduction and Larval Occurrence of the Bottom Invertebrates in the Sound.

The investigations on bottom animal larvae summarised in the present paper are based upon regular plankton samples from the Sound, taken off Ven (3 years) and off Helsingør (1 year). During the first year of the Ven-investigation our experience concerning the identity of the larvae was small, and the counting of the larvae not entirely exact. Hence no graphs, but only a table (p. 372), is given for this year, while the numbers for the two last years for Ven and the one year for Helsingør are given below. — The total number of larvae of bottom invertebrates which have been assorted and referred to their species during these three years is about 177,000 distributed as follows:

	Off Ven. $^{21}/_{8}$-37 to $^{18}/_{8}$-39, 45 main series	Off Helsingør. $^{17}/_{9}$-41 to $^{5}/_{9}$-42, 20 main series	Total
Echinoderms	1,148	2,286	3,434
Polychaetes	15,265	4,324	19,589
Prosobranchs	13,602	7,303	20,905
Tectibranchs	1,966	1,178	3,144
Ascoglossids	256	1,865	2,121
Nudibranchs	491	835	1,326
Lamellibranchs	67,271	36,192	103,463
Cyphonautes	4,156	17,934	22,090
Other larvae	567	563	1,130
Total...	104,722	72,480	about 177,000

If to this number we add all the larvae examined during the first year at Ven and during the detailed investigations within the summer-months, it can be estimated that the material for the present paper is based on direct observations on about $^{1}/_{4}$ million of larvae.

1. The Main-Series, their Value, and their Components.

During the first part of our investigation (at Ven up to $^{10}/_{5}$-38) each main-series was based upon 10 vertical hauls, while the main-series taken at Ven after this date and all the main-series taken off Helsingør include only 5 vertical hauls each. In order to make all the main-series directly comparable, all the 5-haul-series have been multiplied by two in the lists. Each date in the list and in the graphs figs. 193 and 194 thus refers to the total number of larvae per 10 vertical hauls. The diameter of the net used for collecting the main-series was 25 cm, and accordingly 10 vertical hauls will comb the water column over $^1/_2$ sq.m of bottom. The filtration by the net (gauze No. 12) is very good, and it would seem that only a small part of the water mass before the net escapes the process of filtration. The pump-series from Ven, in which 100 or 200 litres of water were pumped up from each m of the water column between the surface and the bottom, and the content of animals examined (cf. pp. 381—392) give us a possibility for checking the efficiency of our vertical hauls (main-series). The 5 pump-series contained the following numbers of larvae calculated for the water column over 1 sq.m of bottom: July 12,700 and 7,000, August 75,000 and 7,700, and September 15,200. If we are to calculate the average number of larvae in these series in order to compare them with the contents of larvae in the main-series, it will be necessary to disregard the 75,000 larvae from August, as this pump-series was on purpose taken during a large maximum of *Polydora ciliata* (totally dominating the pump-series in question) which was characteristic of the plankton during these few days, but which does not normally occur in large numbers during these months. As, furthermore, none of the 15 main-series present from Ven from July to September contained the slightest trace of such a *Polydora*-maximum, the results seem to be incomparable when the pump-series in question is included. A comparison between the four regular pump-series and the 15 regular main-series from July to September taken off Ven gives the following results, in which all the figures are calculated for the whole water column covering 1 sq.m of bottom:

	July	August	September	Average number of larvae
Pump-series	12,700	7,700	15,200	about 10,500
	7,000	..	..	
main-series (net hauls)	45,312	17,488	9,000	
	33,096	12,236	28,762	
	8,432	7,012	2,740	about 11,000
	8.344	6,120	2,178	
	..	3,896	2,070	
	..	3,416	..	

Although the number of pump-series is inconsiderable, the figures seem to show that the results arrived at when using pump and net hauls lie within the same order of magnitude, i. e. the efficiency of the net hauls is very large, and the larval stock captured is really representative of the whole water column through which the haul was made. — Still it must be remembered that the figures given below are minimum numbers for the water column in question.

The time spent on the sea to procure the 10 vertical hauls of a main-series is about $^3/_4$ to 1 hour, and as the current in the Sound moves rather swiftly (off Ven on an average about $^1/_2$ to 1 knot, off Helsingør about 1 to 2 (3) knots), the hauls are distributed over such large water areas that local crowding of larvae seems to be without any influence on the main results. It is known that e. g. Polychaete larvae may occur in swarms along the Indian coasts

(Aiyar 1933, p. 1), but by the method used here, this source of error in the calculations seems to be excluded or at least very much reduced.

The average number of larvae per main-series (10 vertical hauls) in our samples is about 5,500, viz. 4,000 off Ven, and 7,500 off Helsingør, and our results show that our main-series of 10 or 5 hauls give a completely satisfying representation of all the larvae which are of regular and common occurrence in the Sound. However, such larvae as are relatively "rare" in the Sound may often be overlooked or not caught at all. The specialist who finds a single larva of an uncommon larval species among the large larval swarm in his Petri dish, will often be inclined to designate this larva as "rare", forgetting that the apparantly large material at his disposal represents the water column over $^1/_2$ sq.m of bottom only, i. e. a small volume of the huge water masses within the whole area examined.

The large number of supplemental series taken during our investigations have shown that the planktonic larvae — even those which only occur in small numbers — seem as a rule to be distributed very equally throughout the water masses (crowding in swarms seems for most species to be very rare in the Sound). Off Ven our vertical hauls were taken from 18 to 0 m, and 18 m is very nearly the average depth of the Sound north of Taarbæk -Barsebäckshamn (the largest area of the bottom occurs at a depth of 15—25 m, Brattström 1941, p. 31). This means that a similar number of larvae to that found in the water column over 1 sq.m bottom at a depth of 18 m off Ven may on an average be expected to occur over every sq.m of bottom throughout the northern and middle parts of the Sound. The bottom of this part of the Sound has an area of about 800,000,000 sq.m (see the remarks on pp. 23—25)! During the collecting of the two years' main-series off Ven only 3 specimens of larvae of the sea-urchin *Strongylocentrotus droebachiensis* were met with, i. e. 0.26 per cent of all the Echinoderm-larvae and 0.003 per cent of all the bottom animal larvae from all the main-series taken in these two years. From the collections at hand it seems justifiable, therefore, to regard the larva of *Strongylocentrotus* as "rare" in the Sound. Experience has shown, however, that the few *Strongylocentrotus*-larvae actually present were probably equally distributed in the water masses. Our 3 larvae originate from 2 main-series, i. e. from the water column over 1 sq.m of bottom, and if the water column over each sq.m of bottom throughout the Sound contained on an average a similar number of larvae, and this seems likely, the answer will be that within this two year-period the Sound has harboured 3 × 800,000,000, viz. about two and a half milliards of this larva, which judging from our Petri dishes may be assumed to be "rare". During the same two years a single larva of *Echinus acutus* (not known from the Sound in the adult stage) was seen in our main-series. When equally distributed in the water masses, the larvae of this species may on the date in question nevertheless have occurred in more than one and a half milliard spms. in the Sound. Several examples of such "rare" larvae are also met with in the Sound within other groups than the Echinoderms. Thus, for instance, the material of the main-series collected in the Sound contained only 2 larvae of *Acmaea testudinalis*, 5 larvae of *Triphora perversa*, 3 larvae of *Pyrgiscus rufus*, 5 larvae of *Velutina velutina*, 1 larva of *Mangelia attenuata*, and 1 larva of *Philbertia linearis* (all Prosobranchs), 1 larva of the Opisthobranch *Actaeon tornatilis* and — among the Polychaetes — 2 larvae of *Chaetopterus variopedatus* and 1 larva of *Owenia fusiformis*. In spite of their small number in the main-series, all these larvae have undoubtedly been present in considerable numbers throughout the Sound. — If, now, larvae of a certain species are suspended in the water masses in such a way that for instance only one larva is present in the water mass covering 10 sq.m of bottom, we shall only have a 5 per cent chance of catching this larva in a main-series with 10 vertical hauls. And such larvae may nevertheless be present in the Sound in 80 million specimens. — However, experience has shown that such larvae actually occur in the Sound. Young bottom animals (e. g. *Porcellana, Solaster endeca*) have settled and metamorphosed in our bottle-collectors off Ven. Their larvae, however, though known to be pelagic, have never been taken in our main-series. Bottle-collectors exposed off Ven rather frequently contained young bottom stages of *Chaetopterus variopedatus* but the larvae of this species have never been taken in our 3 years' main-series off Ven. Adult specimens of the Echinoderms *Ophiura texturata* and *Ophiopholis aculeata* are very common locally in the Sound; their larvae, however, though known to be pelagic and easily recognisable, have not been met with in our plankton hauls either off Ven or off Helsingør.

When larvae which are rare in our main-series may occur in such large numbers in the water masses, it seems obvious that the dominating larvae in our main-series occur in the Sound in numerous specimens. The total numbers of dominating larvae in the Sound, estimated from the numbers taken on the days on which they were most frequent, are e. g.: *Polydora ciliata* 3,700 to 2,900 milliards; *Polydora coeca* 10,500 to 3,200 milliards; *Littorina littorea* 12,000 to 7,500 milliards; *Mytilus edulis* about 4,500 milliards, and *Cyphonautes* about 2,600 milliards of larvae (all estimated exclusively from the main-series taken off Ven).

In spite of the immense figures given for the last-mentioned species it will be seen that the dominants as well as the larvae which are of very "rare" occurrence in our main-series must be assumed to occur in milliards throughout the Sound. No doubt they all occur in sufficiently large numbers to recruit a population on the bottom, provided that conditions are favourable for their metamorphosis and settling.

Another point which must be kept in mind when using and comparing the figures from our main-series, is the fact that the duration of the larval life may vary from species to species and even within the individual species according to the temperature, the amount of food present, etc. (cf. further pp. 451—457). Our main-series have as far as possible been taken at regular intervals, viz. every two or three weeks all the year round. — Let us imagine that a sudden intense spawning adds a large number of larvae of a certain species to the plankton, and let us set up three possibilities for their pelagic life:

A. The larvae will metamorphose and leave the plankton after a few days or even hours (*Spongia*-larvae, *Hydrobia ulvae*-larvae, larvae of certain Nudibranchs, larval Serpulids, etc., cf. pp. 435—436).
B. The larvae will spend about 10—14 days in the plankton (e. g. the Polychaetes *Eulalia viridis* and *Capitella capitata*, cf. p. 453).
C. The larvae will spend about one month or more in the plankton (f. i. *Polydora ciliata, Owenia fusiformis, Asterias rubens, Ophiocomina nigra, Ophiopholis aculeata, Echinocyamus pusillus, Nassa reticulata, Littorina littorea, Crangon crangon, Leander fabricii* (cf. p. 453).

Larvae of type A — when at all present — will normally only be found in a few scattered specimens in our plankton hauls and will be almost totally overlooked in a main-series. Larvae of type B will only be caught and registered in a single main-series, as they will have disappeared from the plankton before the next main-series sets in. Larvae of type C, however, will often be taken in two (or more) successive main-series, i. e. the same larval maximum will be registered two times in our lists and will accordingly give twice as large a figure as a similar number of larvae of type B in the plankton. — The types B and C within the pelagic larvae and their occurrence in the Sound is discussed in detail on pp. 432—435. A true picture and reliable data on the duration of their larval life, however, are only available for a few forms, but since their larval life seems on an average to be nearly equally long in the species examined of all the larger groups which have a long, pelagic, planktotrophic life (cf. p. 455), the figures given by the graphs will probably not be very far from the average.

Table giving an estimate of the number of larvae of bottom invertebrates in our main-series taken off Ven, depth 18—0 m, from August 1936 to August 1937.

Main-series, Ven August 1936 to August 1937	$^{25}/_{8}$	$^{12}/_{9}$	$^{26}/_{9}$	$^{17}/_{10}$	$^{1}/_{11}$	$^{14}/_{11}$	$^{6}/_{12}$	$^{19}/_{12}$	$^{9}/_{1}$	$^{31}/_{1}$	$^{21}/_{2}$
Echinodermata	++	(+)	+++	+++	+	(+)	(+)	(+)	0	0	0
Polychaeta.......................	++	++	++	?	?	++	+	(+)	(+)	++	+
Prosobranchia....................	+++	++	++	++	+	(+)	(+)	(+)	(+)	0	(+)
Tectibranchia and *Ascoglossa*	++	++	++	+++	+	+	++	+	+	0	(+)
Lamellibranchia	+++	+	++++	?	+++	+++	++++	++	+	(+)	(+)
Other larvae	++	(+)	++	+++	++++	+++	+++	++	+	(+)	(+)

Main-series, Ven August 1936 to August 1937	$^{14}/_{3}$	$^{4}/_{4}$	$^{18}/_{4}$	$^{2}/_{5}$	$^{23}/_{5}$	$^{6}/_{6}$	$^{21}/_{6}$	$^{3}/_{7}$	$^{23}/_{7}$	$^{2}/_{8}$	$^{9}/_{8}$
Echinodermata	0	0	+	+	+	+	0	(+)	(+)	0	+
Polychaeta.......................	+++	++	+++	+++	+++	+++	++	+	+	+++	++++
Prosobranchia....................	(+)	(+)	+	+	+	++	+++	+++	+++	+++	+
Tectibranchia and *Ascoglossa*	(+)	(+)	+	(+)	+	+	+	(+)	+	++	++
Lamellibranchia	(+)	(+)	(+)	+	+++	+++	++++	++++	+++	+++	++++
Other larvae	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	+	+	(+)

++++ = extremely common (more than 1000 larvae). +++ = very common (100—1000 larvae). ++ = common (50—100 larvae). + = not common (10—50 larvae). (+) = rare (1—10 larvae).

Figs. 193 and 194 give the graphs for the total amount of bottom animal larvae per main-series taken off Ven and off Helsingør respectively, and for the individual components, i. e. the individual groups of larvae from which the graphs have been constructed (cf. also the table given above).

Graphs from Ven (cf. pp. 374—375, fig. 193, and the table p. 372). The graph for all the larvae from the two-year-period August 1937 to August 1939, based on about 105,000 larvae, shows the largest maximum in the actual summer (July), but also the spring (April to May) and the winter (December to January) have distinct maxima. The most pronounced minima are normally found in the late autumn (October to November) just before the winter maximum sets in, and in March, when the winter maximum is over. The results of the graphs are further supported by those of table p. 372, referring to the first year off Ven, from which no exact figures are available.

The Polychaete larvae, constituting about 15 per cent — like the Prosobranch-larvae — have one distinct maximum per year. However, this occurs in spring (March to May) and is apparently quite independent of the maxima found for Lamellibranchs and Prosobranchs.

In addition to this maximum, which seems to be constant from year to year, other spontaneous and varying maxima may suddenly appear at any time of the year. They all consist of *Polydora*-larvae, which on account of their special mode of feeding thrive well in the plankton also outside the normal "seasons". Within the larvae of Polychaetes the Spionid-larvae are absolutely dominant, especially the larvae of *Polydora ciliata* and *Polydora coeca*, constituting together 69 per cent of all the Polychaete-larvae found off Ven.

The Prosobranch-larvae, about 15 per cent of the total amount of larvae, have only one maximum per year, appearing rather suddenly and distinct in the actual summer time (June to July) and decreasing during the early autumn. By far the larger number of Prosobranch-larvae belong to *Littorina littorea* and *Nassa reticulata*. During the winter and early spring the larval Prosobranchs disappear almost totally from the plankton, at any rate they are of no significance at all.

The Tectibranchs, constituting about 2 per cent, have their maximum occurrence in July to August. The summer maximum consists mainly of larvae belonging to the Tectibranchs proper, while the Ascoglossids (here included in the graph for Tectibranchs) seem to be somewhat more frequent in the winter, though only rather few specimens per main-series.

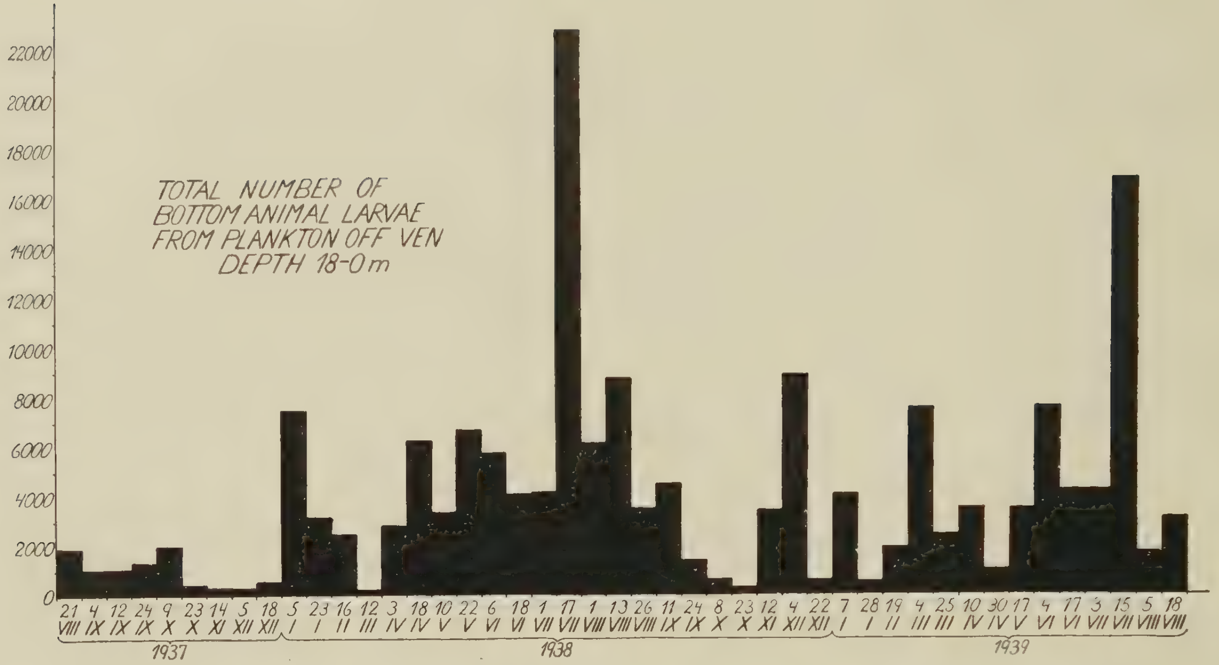
By far the largest amount of the larvae — about 63 per cent — should be referred to the Lamellibranchs, which rather closely follow the summer as well as the winter maxima (but not the spring maximum) given in the graph above. The summer maximum consists of a large number of species with the *Mytilidae* as the dominating element; the winter maximum consists of a smaller number of species with *Mya truncata* as the absolute dominant (see further the table p. 311 and the remarks p. 407).

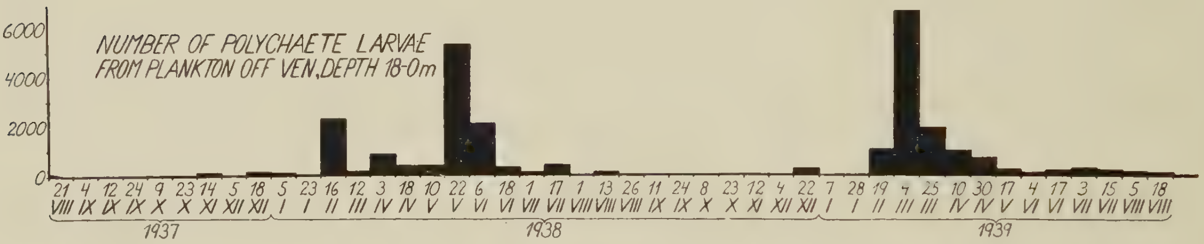
The Echinoderm-larvae, constituting only 0.8 per cent of the total amount of larvae, are of such slight importance in the plankton that their number will hardly appear from the graph when compared with the graphs for the other groups of larvae on the same scale. Their maximum occurrence, however, is in September to October.

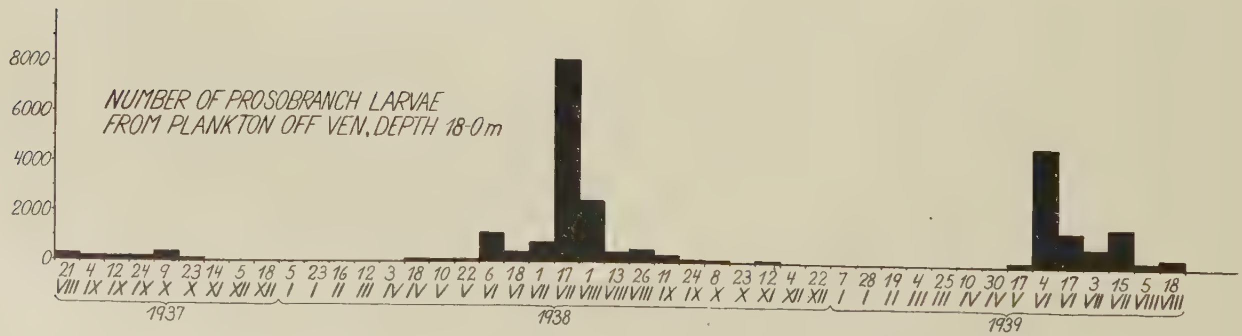
All the other larvae of bottom invertebrates, constituting together 4.5 per cent of the total amount of larvae, are of little importance in the plankton. Among these larvae, comprising Decapods, Balanids, Nudibranchs, Actinians, *Pilidium*, *Phoronis*, and *Cyphonautes*, the larvae of *Cyphonautes* are by far the most numerous (3.5 per cent of the total number of larvae), and have their maximum occurrence in the late autumn, viz. October to December.

Graphs from Helsingør (cf. p. 377, fig. 194). The graph from September 1941 to September 1942, based on about 73,000 larvae, gives in broad features similar results to those from Ven with maxima in summer as well as in winter and spring. The components of these maxima, however, differ rather much from those found off Ven. Especially the number of *Cyphonautes*-larvae taken off Helsingør (24 per cent of the total number of larvae) is sometimes so large that they may dominate a whole main-series. Thus, on $^{11}/_{11}$-41, when the largest number of larvae in a main-series during all our investigations in the Sound, viz. 33,000, was reached, the *Cyphonautes*-larvae constituted 18,400 of these, and on $^{19}/_{12}$-41 *Cyphonautes* larvae were estimated at 6,100 out of the 11,000 larvae present in the main-series. When, however, the number of *Cyphonautes*-larvae is disregarded, the graphs show nearly the same tendencies as those from Ven.

The Polychaete-larvae, about 6 per cent, are much less important than off Ven, but as near Ven, their maximum occurrence is in spring (March), and Spionids, with the genus *Polydora* as the most frequent element, are absolutely dominant.


TOTAL NUMBER OF BOTTOM ANIMAL LARVAE FROM PLANKTON OFF VEN DEPTH 18-0 m
22000
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
21 VIII
4 IX
12 IX
24 IX
9 X
23 X
14 XI
5 XII
18 XII
5 I
23 I
16 II
12 III
3 IV
18 IV
10 V
22 V
6 VI
18 VI
1 VII
17 VII
1 VIII
13 VIII
26 VIII
11 IX
24 IX
8 X
23 X
12 XI
4 XII
22 XII
7 I
28 I
19 II
4 III
25 III
10 IV
30 IV
17 V
4 VI
17 VI
3 VII
15 VII
5 VIII
18 VIII
1937
1938
1939


NUMBER OF POLYCHAETE LARVAE FROM PLANKTON OFF VEN, DEPTH 18-0 m
6000
4000
2000
0
21 VIII
4 IX
12 IX
24 IX
9 X
23 X
14 XI
5 XII
18 XII
5 I
23 I
16 II
12 III
3 IV
18 IV
10 V
22 V
6 VI
18 VI
1 VII
17 VII
1 VIII
13 VIII
26 VIII
11 IX
24 IX
8 X
23 X
12 XI
4 XII
22 XII
7 I
28 I
19 II
4 III
25 III
10 IV
30 IV
17 V
4 VI
17 VI
3 VII
15 VII
5 VIII
18 VIII
1937
1938
1939


NUMBER OF PROSOBRANCH LARVAE FROM PLANKTON OFF VEN, DEPTH 18-0 m
8000
6000
4000
2000
0
21 VIII
4 IX
12 IX
24 IX
9 X
23 X
14 XI
5 XII
18 XII
5 I
23 I
16 II
12 III
3 IV
18 IV
10 V
22 V
6 VI
18 VI
1 VII
17 VII
1 VIII
13 VIII
26 VIII
11 IX
24 IX
8 X
23 X
12 XI
4 XII
22 XII
7 I
28 I
19 II
4 III
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10 IV
30 IV
17 V
4 VI
17 VI
3 VII
15 VII
5 VIII
18 VIII
1937
1938
1939

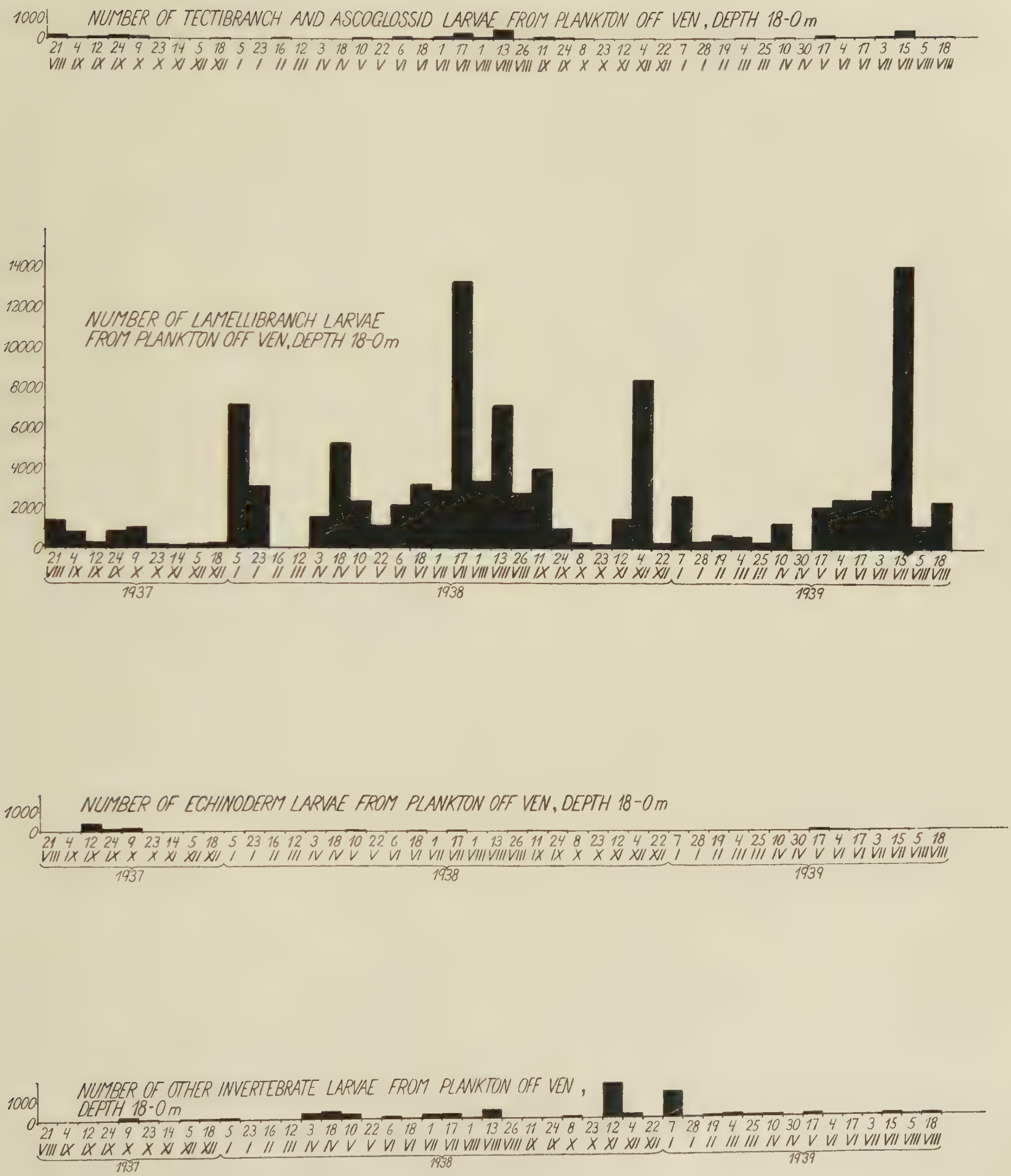


Fig. 193. Graphs showing the varying number of larvae of the different groups of invertebrates in the main-series taken off Ven from $^{21}/_{8}$-1937 to $^{18}/_{8}$-1939.

The Prosobranch-larvae, about 10 per cent, agree rather closely with the results obtained from Ven. Only one maximum per year is found, viz. in the summer (July). Dominants are *Littorina littorea* and *Nassa reticulata*, and from December to March the plankton is nearly free from Prosobranch-larvae.

The Tectibranch-larvae have their maximum occurrence off Helsingør in summer, and the Ascoglossids in late autumn and winter (maximum in November), but these two groups constitute only 4.1 per cent of the total number of planktonic larvae.

The Lamellibranch-larvae taken off Helsingør, about 51 per cent of the total number of larvae, show a winter maximum as early as November with *Mya truncata* as the dominant species, and a summer maximum from June to August dominated by *Mytilidae* and several other forms. The spring maximum found on $^{10}/_{4}$-42 has no parallel within the Ven-series, but is probably an outpost of the large summer spawning induced by the sun's heating of the very shallow water for a few days. As, however, this "maximum" is based upon one main-series and has been observed in a single year only, it will not be dealt with in detail here.

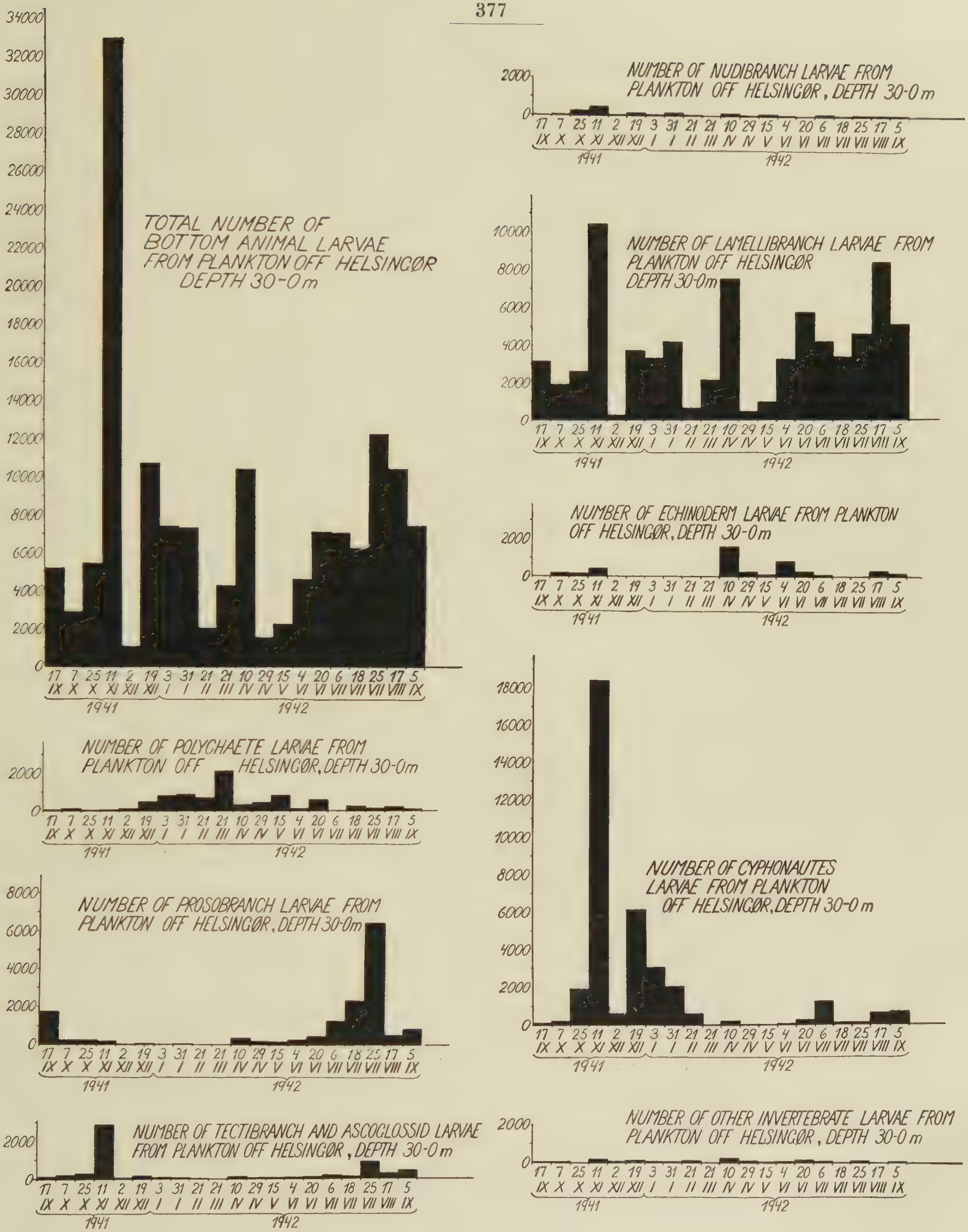
The Echinoderm-larvae, about 3.2 per cent, are also of little importance here, though not so sparse as off Ven. The largest number per main-series was taken on $^{10}/_{4}$-42 (consisting exclusively of larvae of *Ophiura robusta*), but — as off Ven — most of the species of larval Echinoderms occur in late summer and early autumn.

All the other larvae of bottom invertebrates, comprising Decapods, Balanids, Nudibranchs, Actinians, *Pilidium*, and *Phoronis*, constitute together only 2 per cent of the total number of larvae, and the graphs show no real maxima for these groups.

2. Comparison of the Number of Larvae found off Ven and off Helsingør.

As already mentioned, the average number of larvae per main-series is 4,000 off Ven and 7,500 off Helsingør, viz. nearly twice as large in the latter locality, which is in good agreement with the depth of the water-columns (18—0 m and 30—0 m respectively) through which the hauls were made. However, as far as I can see, this large number taken off Helsingør must to a large extent be ascribed to the larvae entering the Sound from the Kattegat. As these Kattegat larvae constitute a vital element for the fauna of the Sound, it seems justifiable to consider this question in detail here.

The Sound contains (as mentioned on pp. 23—25) two water layers: A Baltic water layer (8 to 15 m thick), normally forming the surface layer and flowing towards the north, and a Kattegat layer, occupying the whole volume beneath the Baltic layer and normally entering the Sound from the north. The pump-series (pp. 381—393) and other experiences have shown that the boundary between these two layers is very distinct, also as regards the larvae, which are often very sensitive to changes in the temperature and salinity. Thus each of the two layers contains its special stock of larvae. The Baltic layer especially in summer contains large quantities of small larvae originating from parents in the Sound itself or the adjacent parts of the Baltic. The number of larvae contained in this layer, though generally a few metres thicker off Helsingør than off Ven (cf. p. 24), seems to be nearly the same in both the localities examined. The only larva closely associated with the Baltic water layer which has been registered with absolute certainty during the whole investigation is that of *Littorina littorea*, the parents of which are frequent throughout the Sound from Amager—Limhamn to Kullen—Gilleleje. The larvae of this species show the following figures:



TOTAL NUMBER OF BOTTOM ANIMAL LARVAE FROM PLANKTON OFF HELSINGØR DEPTH 30-0 m

NUMBER OF NUDIBRANCH LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0 m

NUMBER OF LAMELLIBRANCH LARVAE FROM PLANKTON OFF HELSINGØR DEPTH 30-0m

NUMBER OF ECHINODERM LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0 m

NUMBER OF POLYCHAETE LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0m

NUMBER OF CYPHONAUTES LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0 m

NUMBER OF PROSOBRANCH LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0m

NUMBER OF TECTIBRANCH AND ASCOGLOSSID LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0 m

NUMBER OF OTHER INVERTEBRATE LARVAE FROM PLANKTON OFF HELSINGØR, DEPTH 30-0 m

34000
32000
30000
28000
26000
24000
22000
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
17 7 25 11 2 19 3 31 21 21 10 29 15 4 20 6 18 25 17 5
IX X X XI XII XII I I II III IV IV V VI VI VII VII VII VIII IX
1941
1942

Fig. 194. Graphs showing the varying number of larvae of the different groups of invertebrates in the main-series taken off Helsingør from $^{17}/_{9}$-1941 to $^{5}/_{9}$-1942.

Off Ven, August 1937 to August 1938, average of 23 main-series: 527 larvae per main-series.

Off Ven, August 1938 to August 1939, average of 22 main-series: 400 larvae per main-series.

Off Helsingør, Sept. 1941 to Sept. 1942, average of 20 main-series: 431 larvae per main-series.

The figures seem to support the conjecture that the larvae of *Littorina* are equally frequent off Ven and off Helsingør, and as these larvae are some of the commonest larvae within the Baltic layer and belong to the dominant animals here, it seems reasonable to suppose that the content of bottom animal larvae within the Baltic layer is on the whole of the same order of magnitude off Ven as off Helsingør.

If I am right in this conclusion, the result must be that the increasing number of larvae in the main-series from Helsingør as compared with those from Ven should be referred nearly exclusively to the large number of larvae in the Kattegat layer. While the Baltic layer shows only small variations in thickness throughout the Sound, the Kattegat layer has a greatly varying thickness according to the depth of the locality (cf. e. g. the different average depths off Ven (18—20 m) and off Helsingør (about 30 m or somewhat more) from which our main-series were taken). The volume (the water column) of Kattegat water sieved by our plankton nets off Helsingør is therefore more than twice as large as that sieved off Ven, while the volume of Baltic water sieved in the two localities is nearly just as large or inconsiderably larger in the former locality. Hence, if on the same day the Kattegat water contains the same number of larvae per cubic metre off Ven and off Helsingør, the number of larvae contained in a plankton series off Helsingør must be twice as large as off Ven, as has also proved to be the case.

The Kattegat water, however, enters the Sound from the north in a nearly constant stream, and the fact that the same number of larvae per cubic unit occur in the Kattegat water off Helsingør as off Ven in spite of the much thicker layer of Kattegat water in the former locality, seems to show that a large proportion of the larvae off Helsingør have been transported to the Sound from the Kattegat.

Dredge hauls and bottom samples have shown that the fauna of adult bottom invertebrates living in and washed by the Kattegat water seems to be just as rich in adult specimens off Ven as off Helsingør, i. e. the number of eggs shed and larvae produced by the parent stock in the two localities is of about the same order of magnitude. Since the Kattegat water moves southwards, no larvae from parents off Ven may be stored in the Kattegat water farther northward in the Sound. If, therefore, the larvae contained in the Kattegat layer off Helsingør originated from parents in that locality, the number of larvae per cubic unit off Helsingør would be much smaller than off Ven, where the stock of larvae produced is stored up in a much smaller water volume and is accordingly much more concentrated. As has been shown, however, this is not the case; the water mass off Helsingør comprises a large number of extra larvae, which have, no doubt, been carried to the Sound from the Kattegat.

The fact that several species of larvae in this water mass are always met with in late stages only, seems likewise to support the conjecture that they originate from the Kattegat and not from the Sound itself (cf. pp. 390—391). If I am right in the conclusions given above, it will be seen that the number of larvae carried to the Sound from the Kattegat is astonishingly large. Thus, off Helsingør 50 per cent (or probably much more, cf. p. 390) of all the bottom animal larvae seem to originate from parents in the Kattegat. The fact that such Kattegat-larvae (judging from the predominance in several species of late larvae) are also present off Ven, where we are unable to state their number at present, seems to show that this percentage has been estimated too low, and I think it will be very near the truth to assume that about 50 per cent of the whole stock of larvae in the northern and middle parts of the Sound originate from parents in the Kattegat. This is strongly supported by the results obtained from our pump-series (cf. pp. 390—391). Eggs and larvae shed by parents from the deeper areas of the Sound itself will often be carried southwards and will perish there when they are exposed to the Baltic water.

3. Fluctuations in the Number of Larvae from Year to Year.

The stock of larvae in the water masses of the Sound may vary considerably from year to year. The curves in fig. 195 give the contents of larvae in the main-series from Ven during the period May to December for the years 1937, 1938, and 1939 (the latter ending in September). It is seen that the number of larvae is very high for 1938: on an average 5,300 larvae per main-series for the whole year, and that the figures for 1939 seem to follow those from 1938 rather closely. The curve for 1937: on an average 925 larvae per main-series (only reckoned from May to December), gives an entirely different picture although the main-series were taken with the same net in the same locality. The number of larvae in 1938 was four to five times as high as that from 1937. What is especially characteristic is the small maximum of the "Baltic spawning" in 1937 as compared with the distinct maxima in 1938 and 1939.

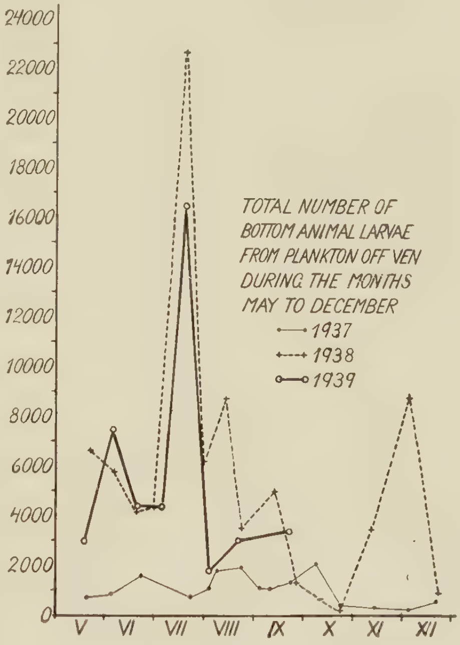


Fig. 195. Cf. the text on p. 379.

One of the reasons for this small number of "summer-larvae" in 1937 is probably to be found in the fact that January, February, and March 1937 were very cold with very large ice masses in the Sound. Such an ice-winter is known to kill large numbers of the animals living in shallow water (Aurivillius 1885, Blegvad 1929, Gustafson 1942, Smidt 1944a). The mortality is especially high for the more sedentary species as for instance *Mytilus edulis*, *Cardium edule*, and *Mya arenaria*, while a species like *Littorina littorea* will normally be able to escape to somewhat deeper water below the ice-crust. The Lamellibranchs mentioned, however, are producers of some of the most dominant larvae within the Baltic spawning, which will accordingly be reduced in the summer after a heavy ice-winter. Similar results seem to be obtained from the main-series taken off Helsingør in the summer of 1942 (cf. the graphs in fig. 194), — a summer which followed upon one of the coldest winters for the last hundred years.

However, the curves in fig. 195 are somewhat "unjust" as to the year 1937. The maximum, which in the 1938-curve is seen at the beginning of December, in the previous year was not recorded till January 1938 and is thus not included in the 1937-graph above.

If we compare the number of larvae per main-series from the two last years taken off

Ven, viz. $^{21}/_{8}$-37 to $^{13}/_{8}$-38, and $^{26}/_{8}$-38 to $^{18}/_{8}$-39 respectively, we shall obtain the following figures:

Group / Year	$^{21}/_{8}$-37 to $^{13}/_{8}$-38. Average of 23 main-series	$^{26}/_{8}$-38 to $^{18}/_{8}$-39. Average of 22 main-series
Echinodermata	45	18
Polychaeta	580	604
Prosobranchiata	650	495
Tectibranchiata	86	53
Ascoglossa	8	10
Nudibranchiata	20	12
Lamellibranchiata	2,548	2,384
Cyphonautes	100	176
Balanus	18	23
Other larvae	2	6
Total...	4,057	3,781

It will be seen that the figures for the Polychaetes and the Lamellibranchs as well as for the total number of larvae per main-series are very similar for the two years, and also the figures for the third large group of larvae, viz. the Prosobranchs, agree fairly well for the two years. A greater agreement between the numbers of larvae for two successive years than that found here can hardly be expected considering the methods of collecting employed. It can therefore be taken for granted that the curves for 1938 and 1939 are characteristic of the Sound under normal conditions, i. e. when no larger ice masses occur in the Sound during the winter.

The year 1938, which as to the Baltic spawning and the main part of the Kattegat spawning seemed to be a normal year, showed quite abnormal conditions for the Echinoderm-larvae. As mentioned above these larvae are never very numerous in the Sound plankton, but by far the largest number of them are associated with the Kattegat layer and have their maximum occurrence in the early autumn, especially in the months September—October. The following data can be stated as to the number of Echinoderm-larvae in the autumn plankton taken off Ven in the different years:

September—October 1936: Hundreds of larvae per main-series. Larvae still numerous on $^{1}/_{11}$, but decreasing in number on $^{14}/_{11}$. No exact figures are available.
September—October 1937: About 150 larvae per main-series (average of 5 main-series).
*September—October 1938: About 35 larvae per main-series (average of 4 main-series).
September 1939: About 200 larvae in the individual main-series.

Of these four years only the year 1938 has a remarkably small number of Echinoderm-larvae, viz. only one-fifth to one-sixth of the numbers found in 1936, 1937, and 1939. The figures from Helsingør for September—October 1941, viz. 125 larvae (average for 3 main-series, and 400 larvae in the main-series from $^{11}/_{11}$-1941) seem to agree well with the number found in normal years off Ven. The possibility, that in 1938 the occurrence of the larvae should have been displaced to another month outside the normal season, is rejected by the fact that the larval number was very small earlier as well as later in the season. The few larvae present in 1938 were in precisely that stage of development which in normal years also is characteristic of the date in question, i. e. a spawning has taken place also in 1938 at the normal time of the year, but this spawning has either been smaller than is usually the case or the spawned eggs or larvae have been subjected to a catastrophe. — Dr. MORTENSEN (1920) observed in Kristineberg-aquaria a couple of males of *Amphiura filiformis* rising above the mud and spawning in the usual way. The sperm, however, sank to the bottom in thick masses, and the spermatozoa did not move at all. The temperature was high enough to induce spawning, but the salinity was too low to activate the sperm, and as spawning in the females is induced by active sperm only, no discharge of eggs took place. The same author (MORTENSEN 1938, p. 11) is on the whole of opinion that a large part of the "waste" in Echinoderm-larvae is due to the lack of fertilisation caused by unactivated spermatozoa (see this paper pp. 445—446). It seems probable that precisely the Sound is a locality in which such a catastrophe may occur, since the Baltic layer will occasionally extend down into areas normally washed by the Kattegat layer. In August—September this Baltic water is warmer (17.3°—14.7° C.) than the Kattegat water (13°—9° C.) (BRATTSTRÖM 1941). The rise of temperature caused by the Baltic water will thus probably stimulate the ripe Echinoderms to spawn, but as the salinity is too low to activate the sperm, the eggs will not be shed, or — if shed — they will not be fertilised. BRATTSTRÖM (1941, p. 90) has shown that "in the year 1938 a heavy decrease in the main salinity from 10 m downwards occurred in the Sound as well as in southern and middle Kattegat" (translated from the German). These remarks are in good agreement with and support the suggestions given above.

4. Distribution of the Larvae in the Water Masses (Pump-Series).

Pump-series have been taken in the months of July, August, and September from the main-station off Ven. The technique used is described in detail on pp. 14—16. Usually 200 to 100 l water were pumped up from each metre of the water column, and the content of bottom animal larvae was carefully examined.

Table showing the temperatures (Centigrade) in the water-column from which our main-series have been taken off Ven. 18 m depths = bottom. Measurements earlier than $^{15}/_{12}$-1937 are not available.

Depth	$^{5}/_{12}$-37	$^{5}/_{1}$-38	$^{23}/_{1}$-38	$^{16}/_{2}$-38	$^{12}/_{3}$-38	$^{3}/_{4}$-38	$^{18}/_{4}$-38	$^{10}/_{5}$-38	$^{22}/_{5}$-38	$^{6}/_{6}$-38	$^{18}/_{6}$-38	$^{1}/_{7}$-38	$^{17}/_{7}$-38	$^{1}/_{8}$-38	$^{13}/_{8}$-38	$^{26}/_{8}$-38	$^{11}/_{9}$-38	$^{25}/_{9}$-38	$^{8}/_{10}$-38
0 m	5.2	0.8	3.4	1.6	3.9	..	5.4	8.4	9.2	12.5	15.1	14.5	16.2	18.7	20.3	17.5	16.6	15.7	12.9
5 m	..	..	..	1.7	3.8	..	..	8.4	9.3	12.5	14.7	14.2	16.0	18.2	20.5	17.4	16.6	15.7	13.2
10 m	..	..	5.5	1.7	3.7	..	5.6	8.2	9.2	12.5	13.7	14.1	15.9	17.5	15.3	17.2	16.7	15.7	11.3
15 m	..	..	6.5	2.0	3.8	..	5.9	7.6	9.6	7.0	11.8	13.9	13.4	10.3	11.6	15.4	12.3	12.2	11.3
18 m	..	9.7	7.4	4.8	3.8	..	5.5	7.2	6.2	6.5	7.1	11.5	8.9	9.9	10.5	11.1	10.8	11.5	13.3

Depth	$^{23}/_{10}$-38	$^{12}/_{11}$-38	$^{4}/_{12}$-38	$^{22}/_{12}$-38	$^{7}/_{1}$-39	$^{28}/_{1}$-39	$^{19}/_{2}$-39	$^{4}/_{3}$-39	$^{25}/_{3}$-39	$^{10}/_{4}$-39	$^{30}/_{4}$-39	$^{17}/_{5}$-39	$^{4}/_{6}$-39	$^{17}/_{6}$-39	$^{3}/_{7}$-39	$^{15}/_{7}$-39	$^{5}/_{8}$-39	$^{18}/_{8}$-39	$^{16}/_{9}$-39
0 m	11.4	10.2	7.5	..	2.5	2.8	2.6	2.8	2.5	4.8	5.8	9.5	14.0	15.3	16.2	16.2	18.5	19.6	17.8
5 m	11.5	10.2	8.0	..	2.8	2.7	3.4	2.8	2.4	4.2	5.8	9.0	13.0	15.1	16.1	16.4	18.3	19.4	17.9
10 m	11.5	10.2	9.3	..	4.0	3.0	3.6	2.8	2.3	4.6	5.9	7.6	12.6	15.1	9.5-12.3	16.4	18.2	18.4	15.0
15 m	11.5	10.3	11.1	..	7.7	6.3	4.0	4.9	4.4	5.2	6.6	6.0	6.3	12.8	14.3	15.2	16.8	13.1	11.0
18 m	12.0	10.7	7.4	..	8.0	7.5	4.7	6.2	5.0	5.2	6.0	5.8	6.2	7.3	7.4	8.5	9.6	9.1	11.0

As already described on pp. 23—25, the spring-layer between the Baltic water and the Kattegat water may vary, the Baltic layer being from 8 to 15 m thick. The table on p. 381, which gives the temperatures in the water column off Ven during two years, shows clearly that the spring layer is normally found at depths between 10 and 15 m. Careful observations of the temperature for each metre of the water column from the surface to the bottom (16—19 m) were made off Ven contemporaneously with the five pump-series. According to these measurements the spring-layer seems to occur at a depth of 8—9 m, 9—10 m, 9—10 m, 10—13 m, and 10—14 m respectively, and these and several other experiences seem to show that the Baltic water layer is somewhat thinner off Ven than in the northernmost, deeper part of the Sound, but no great difference is found.

Unfortunately only temperature measurements, but no measurements of the salinity were made; such measurements would have been of value if we are to give the exact depth of the spring layer. Here, however, our observations during several years of the behaviour of the different larval species have helped us to clear up the problem. Several of the larvae which in our pump-series were found in the uppermost few metres of the water column with a distinctly decreasing temperature (as compared with the surface temperature) have been kept in aquaria or taken to the laboratory in Dewar vessels, and proved only to survive in water of a salinity of 20 $^0/_{00}$ or more. When placed in water of a lower salinity, they died in a few hours. This is for instance the case with the larvae of *Echinocyamus pusillus*, *Aporrhais pes pelecani*, and *Phoronis mülleri* (all found at a depth of 10 m on $^{27}/_{7}$ 1937), *Montacuta bidentata* and *Eulimella nitidissima* (both found at a depth of 10 m on $^{22}/_{8}$ 1937), and *Echinocyamus pusillus*, *Anomia squamula*, and *Cultellus pellucidus* (all found at a depth of 9 m on $^{25}/_{9}$ 1937). These species of larvae seem exclusively to be associated with the Kattegat water, and as, further, their uppermost occurrence in the water column corresponds to the depth at which a heavy decrease in the temperature sets in, it seems reasonable to regard this depth as the boundary between the two water layers in question. Although these two layers are fairly well separated, there are, of course, a few metres in a vertical direction in which a mixed water mass may occur. It is, however, a well known fact that while the Baltic larvae are able to thrive in both water masses, the larvae from the Kattegat layer will not thrive at all in the Baltic layer. As, furthermore, the young photopositive larvae (cf. pp. 460—463) of the Kattegat layer must be supposed to crowd as near the surface as the salinity and the temperature allow, i. e. immediately below the Baltic layer, it seems justifiable to designate the water mass extending from the depth at which the first distinctly decreasing temperatures as also the first typical "Kattegat larvae" are met with, to the bottom as "Kattegat water". In the following tables and calculations the terms "Baltic water" and "Kattegat water" are used in accordance herewith.

As no time could be spared for this time-consuming work during the winter, and as our primitive equipment could not defy the winter storms, the pump-series have hitherto been confined to the months of July, August, and September, i. e. to the period in which the two largest spawnings of the year take place in the Sound. The Baltic spawning, which, induced by the sudden rise of the surface temperature, is started late in May or in June, reaches its maximum in July, and decreases during August. The larvae have often nearly totally disappeared from the plankton towards the end of this month, but now and then an "indian summer" with a few young larvae in the plankton will occur early in September. The Kattegat spawning, however, shows the first small tendencies to start in late July or early in August, increasing considerably during this latter month to attain its largest number of species and specimens in September—October (cf. pp. 398—408), which is in good agreement with the rise of the temperature found at depths larger than 20 m from June—July to August—September.

The tables on pp. 384—389, which comprise these two spawnings and give reliable figures concerning their quantitative and qualitative significance in the Sound, show the following details:

The pump-series from the end of July (pp. 384—385) contained 42 species of larvae. Of these, 23 species were found in the Baltic water and 37 in the Kattegat water. The average number of species per 200 l water was on $^{27}/_{7}$-37: 7 in Baltic water and 14 in Kattegat water, and per 100 l water on $^{30}/_{7}$-38: 3 in Baltic water and 8 in Kattegat water. The total number of larvae calculated for the water column covering 1 sq.m of bottom was on $^{27}/_{7}$-37: 12,700, viz. 4,350 (= 34 per cent) in the Baltic layer and 8,350 (= 66 per cent) in the Kattegat layer. On $^{30}/_{7}$-38 the corresponding figures were: total 7,000 larvae, viz. 1,400 (= 20 per cent) in the Baltic layer, and 5,600 (= 80 per cent) in the Kattegat layer. These figures for the number of species as well as for the number of specimens seem on an average to show that the number of larvae and of spawning species at the end of July is twice as large in the Kattegat layer as in the Baltic layer. The Baltic layer has only one large spawning per year (cf. pp. 402—405), commencing in late May or June, but already in late July, when this spawning is still very near its maximum, the Baltic larval stock is only half as large as that of the Kattegat layer. The dominating larvae in the Baltic spawning are those of *Littorina littorea* and "*Mytilidae sp.*", i. e. *Mytilus edulis.* A rope, 30 m long, which had been suspended vertically off Ven from the bottom to the surface for 6 weeks in July and early August 1939, was entirely covered with $^{1}/_{4}$ to $^{1}/_{2}$ million of young *Mytilus* on the upper 10 to 15 m of the line (i. e. the part exposed to the Baltic water), while the lower part, exposed to the Kattegat water, was nearly free from young.

The two pump-series from August (pp. 386—387) will be discussed separately, as the series from $^{12}/_{8}$ and that from $^{22}/_{8}$ showed entirely different figures. The series from $^{12}/_{8}$-37 contained 32 species of larvae, of which 21 were found in the Baltic layer and 23 in the Kattegat layer. The average number of larval species per 100 l was 8 in the Baltic, and 16 in the Kattegat water. The total number of larvae for the water column covering 1 sq.m of bottom was 75,000, viz. 21,000 (= 28 per cent) in the Baltic water, and 54,000 (= 72 per cent) in the Kattegat water. The number of larvae within the Kattegat layer seems thus to be 2 to 3 times as large as that of the Baltic layer. The pump-series from $^{22}/_{8}$-37 shows a quite different picture. The total number of species is 33, of which 7 occurred in the Baltic layer and 33 in the Kattegat layer. The average number of larval species per 100 l was 2 in the Baltic water and 15 in the Kattegat water. The total amount of larvae over 1 sq.m of bottom was 7,700, viz. 500 (= 7 per cent) in the Baltic water and 7,200 (= 93 per cent) in the Kattegat water. The Baltic spawning seems here to be nearly completed, while the Kattegat spawning has increased considerably. The Baltic larvae comprise only about 10 per cent of the whole stock of larvae.

The pump-series from September (pp. 388—389) contained 44 species of larvae, 17 in the Baltic water and 43 in the Kattegat water. The average number of larval species per 100 l in the Baltic water was 4, and in the Kattegat water 15. The total stock of larvae over 1 sq.m of bottom was 15,200, viz. 1,700 (= 11 per cent) in the Baltic layer and 13,500 (= 89 per cent) in the Kattegat layer. In spite of a few laggards of Baltic larvae, the total Baltic larval stock constitutes only about 10 per cent of all the larvae in the plankton, i. e. the stock of Kattegat larvae is entirely dominant.

Dominating larvae in the Kattegat spawning are: *Aporrhais pes pelecani, Nassa reticulata,*

Pump-series taken off Ven, depth 0—18 m (bottom), on July 27th 1937.
were pumped up (cf. the text on p. 383). Larvae with an *

Depth in metres	½	2	3	4	5	6	7	8	9	10	11	12	13
Temperature (Centigrade)	18.0°	18.0°	18.0°	18.0°	18.0°	17.2°	17.9°	17.8°	17.4°	15.9°	14.5°	12.4°	12.1°
Estimate of the volume of Phytoplankton (+) = very poor, ++++ = extremely rich, etc.	(+) *Ceratium*	(+) *Ceratium, Diatoméans*	÷	(+) *Ceratium*	(+) *Ceratium*	(+) *Ceratium*	(+) *Ceratium*	(+) *Ceratium*	(+) *Ceratium*	+++ *Ceratium, Dinophysis, Peridinineans*	++++ *Ceratium, Dinophysis*	++++ *Ceratium*	++ *Ceratium*
Asterias rubens	..	..	..	..	..	..	*1	..	..	..	..	..	..
Echinocardium cordatum	..	..	..	..	..	..	..	*1	..	*6	*1	..	..
Echinocyamus pusillus	..	..	..	..	..	..	..	..	..	2	..	..	..
Amphiura filiformis	..	..	..	..	..	..	..	..	..	..	..	1	..
Littorina littorea	113	33	61	82	43	41	13	18	7	5	9	28	4
Alvania punctura	..	..	..	..	..	..	..	..	..	..	..	..	..
Bittium reticulatum	..	..	..	..	..	..	..	..	..	..	..	..	..
Rissoa sp.	..	3	7	1	1	*8	*8	..	1	..	..	..	..
Odostomia sp.	..	..	..	..	..	..	..	..	..	..	1	..	..
Aporrhais pes pelecani	..	..	..	..	..	..	..	..	..	2	1	2	..
Nassa reticulata	..	..	..	..	..	..	..	..	..	5	9	9	6
Prosobranchiata sp.	1	9	..	..	..	..	..	7	2	3	3	..	2
Philine aperta	..	..	..	1	..	..	3	4	3	8	25	13	4
Acera bullata	..	..	..	..	..	..	..	..	..	..	2	..	5
Retusa umbilicata	..	..	..	..	..	..	..	..	1	3	11	2	4
Limapontia capitata	..	..	..	..	..	..	..	..	..	2	..	..	..
Anomia squamula	..	..	..	..	..	..	..	..	..	..	1	2	..
Lima loscombi	..	..	..	..	..	..	..	..	..	..	..	..	..
Mytilidae sp.	6	16	10	42	29	36	18	12	13	6	5	4	2
Cardium fasciatum	..	..	..	..	..	..	..	1	..	1	5	5	2
Cultellus pellucidus	..	..	..	..	..	..	..	..	..	..	..	..	..
Saxicava arctica	..	..	..	..	..	..	..	..	..	1	..	..	..
Saxicava rugosa	..	..	..	..	..	..	..	..	..	2	..	..	..
Zirphaea crispata	3	1	..	..	..	..	..	..	..	..	..	..	..
Teredo navalis	..	..	..	..	..	..	..	2	..	..	..	..	..
"Oktober-oval"	..	..	..	..	..	..	..	..	..	2	..	..	..
Lamellibranchiata sp.	8	12	18	18	18	135	23	34	15	13	59	68	27
Mya arenaria	20	..	..	..	..	..	..	..	..	..	..	..	..
Harmothoë sp.	..	..	..	..	..	..	..	..	..	..	..	..	..
Polydora ciliata	..	..	..	..	..	3	..	..	..	..	..	..	..
Spionidae sp.	..	..	..	..	..	..	1	..	..	..	..	..	..
Magelona papillicornis	..	..	..	..	..	1	..	..	..	..	..	..	..
Disoma multisetosum	..	..	..	..	..	..	..	..	..	2	..	14	..
Poecilochaetus serpens	..	..	..	..	..	..	..	..	..	..	3	..	..
Pectinaria koreni	..	..	..	..	..	..	1	..	..	5	9	..	..
Polychaeta sp.	..	..	..	..	..	..	1	..	..	3	1	..	6
Balanus, Nauplia	..	..	..	2	..	..	..	..	..	..	..	..	..
Balanus, Cypris	..	..	..	..	..	..	..	..	1	2	2	2	..
Brachyura, Zoëa	..	..	..	..	..	..	..	..	..	1	..	..	..
Cyphonautes	..	..	2	2	(+)	..	1	2	5	10	7	3	5
Phoronis mülleri	..	..	..	..	..	..	..	..	..	1	..	..	..
Actinia sp.	..	..	1	..	..	..	..	..	..	..	..	..	..
Total number of specimens	151	74	99	148	91	224	70	81	48	85	154	153	67
Total number of species	6	6	6	7	5	6	10	9	9	22	18	13	11

Total for the whole pump-series: 40 species.
Total number of larvae in a water column covering 1 sq.m of bottom: 12,700.

The Baltic water contains: 4,350 larvae (= 34 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 22 species (i. e. on an average 7 species per 200 l water).

The Kattegat water cont
total larval stock) in a
bottom, comprising 34 s
per

ch metre 2001 of water ught dead.				Pump-series taken off Ven, depth 0—18 m (bottom), on July 30th, 1938. From each metre 100 l of water were pumped up (cf. the text on p. 383)									
15	16	17	18	3	6	8	10	13	15	16	17	bottom 18 m	
9.1°	8.6°	8.0°	8.0°	18.6°	17.9°	17.5°	17.4°	13.9°	12.2°	10.7°	9.2°		
+++	+	(+)	÷										
Ceratium, Dinophysis	*Ceratium*	*Ceratium*		?	?	?	?	?	?	?	?	?	
..	..	..	*1	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
4	2	..	3	6	8	1	2	..	6	5	11	..	
1	..	..	..	..	..	..	..	..	..	..	..	..	
..	3	1	..	..	..	..	..	..	..	..	1	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
3	1	..	..	..	..	..	..	..	..	..	..	..	
1	..	..	..	2	..	..	..	3	..	..	5	..	
8	..	..	..	..	..	..	..	..	..	..	1	..	
1	..	..	..	..	..	..	..	..	1	..	..	..	
2	..	..	..	..	..	..	..	2	1	..	..	..	
17	9	9	5	..	..	..	1	2	..	1	..	..	
..	..	..	..	..	..	..	..	..	..	..	1	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	1	..	
?	35	60	6	2	1	..	..	15	26	10	38	..	
?	4	3	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	2	1	1	..	
..	..	..	..	..	..	..	..	1	..	..	1	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	6	2	..	..	..	
..	9	8	3	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
500	90	1	..	1	..	1	2	49	52	23	62	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	2	..	..	..	..	..	..	..	..	..	
..	..	..	112	..	..	..	..	..	..	..	7	..	
..	..	1	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	2	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
5	..	2	..	..	..	..	..	..	1	..	..	..	
23	5	..	5	..	..	..	..	..	..	..	2	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	1	1	1	..	..	..	..	..	..	..	..	..	
..	1	..	..	..	..	..	..	..	..	..	..	..	
59	9	4	2	..	..	..	..	..	..	2	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	
624	169	90	142	11	9	2	5	78	91	42	131	..	Total number of spms.
?14	12	10	11	4	2	2	3	7	8	6	12	..	Total number of species
350 larvae (= 66 % of the lumn covering 1 sq.m of e. on an average 14 species ter).				The Baltic water contains: 1,400 larvae (= 20 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 5 species (i. e. on an average 3 species per 100 l water).				The Kattegat water contains: 5,600 larvae (= 80 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 18 species (i. e. on an average 8 species per 100 l water).					Total for the whole pump-series: 18 species. Total number of larvae in a water column covering 1 sq.m of bottom: 7,000.

	Pump-series taken off Ven, depth 0—18 m (bottom), on August 12th, 19 From each metre 100 l of water were pumped up (cf. the text on p. 3 Larvae with an * were caught dead.							
Depth in metres	0	1	2	4	6	7	10	14	1
Temperature (Centigrade)	18.7°	18.8°	18.8°	18.8°	18.9°	19.0°	19.5°	16.3°	10.
Estimate of the volume of Phytoplankton, (+) = very poor, ++ = rather rich, etc.	?	?	?	?	?	?	(+) *Ceratium*	+ *Ceratium*	?
Echinocardium cordatum	*1	. .	. .	. .	. .	. .	. .	*6	. .
Ophiura albida	. .	. .	. .	. .	. .	. .	. .	1	. .
Ophiura sp.	. .	. .	. .	. .	. .	. .	. .	*1	. .
Other *Echinoderm larvae*	. .	. .	. .	. .	. .	. .	. .	1	. .
Littorina littorea	1	41	88	73	15	82	2	. .	. .
Alvania punctura	. .	. .	. .	. .	. .	. .	. .	. .	. .
Bittium reticulatum	. .	. .	. .	3	. .	1	. .	. .	. .
Odostomia sp.	. .	. .	. .	. .	. .	. .	. .	. .	. .
Eulimella nitidissima	. .	. .	. .	. .	. .	. .	. .	. .	.
Aporrhais pes pelecani	. .	. .	. .	. .	. .	. .	. .	. .	
Nassa reticulata	. .	10	12	14	2	5	. .	7	
Prosobranchiata sp.	. .	2	3	. .	. .	. .	1	2	
Philine aperta	. .	. .	. .	. .	. .	. .	2	8	
Philine sp.	. .	. .	. .	. .	. .	. .	. .	. .	. .
Acera bullata	. .	. .	. .	. .	. .	. .	. .	. .	. :
Retusa umbilicata	. .	. .	. .	. .	1	. .	. .	. .	
Limapontia capitata	. .	. .	. .	. .	. .	. .	. .	. .	. .
Elysia eller Stiliger	2	. .	. .	. .	. .	. .	. .	. .	. .
Anomia squamula	. .	. .	. .	. .	. .	. .	. .	. .	
Mytilidae	3	28	58	96	31	51	8	5	
Cardium fasciatum	. .	. .	. .	. .	. .	. .	. .	. .	
Cultellus pellucidus	. .	. .	. .	. .	. .	. .	. .	. .	. .
Saxicava rugosa + arctica	. .	. .	. .	. .	. .	. .	5	. .	. .
Zirphaea crispata	. .	6	7	2	. .	1	. .	. .	. .
Teredo navalis	. .	. .	. .	. .	. .	. .	. .	. .	
Mya arenaria	. .	14	18	. .	. .	5	. .	. .	. .
Montacuta bidentata	. .	. .	. .	. .	. .	. .	. .	9	
Lamellibranchiata sp.	3	290	156	20	41	195	14	67	
Polydora ciliata	12	. .	. .	. .	. .	. .	. .	. .	1,0
Spionidae sp.	. .	1	. .	. .	. .	. .	. .	. .	.
Magelona papillicornis	. .	. .	. .	. .	. .	. .	6	. .	.
Disoma multisetosum	. .	. .	. .	. .	. .	. .	. .	60	.
Pectinaria koreni	. .	. .	. .	. .	. .	. .	1	2	
Polychaeta sp.	. .	. .	. .	. .	1	. .	1	1	.
Nereis diversicolor	. .	. .	. .	. .	. .	. .	. .	. .	.
Balanus, Cypris	. .	. .	. .	. .	. .	. .	. .	. .	.
Brachyura, Zoëa	. .	. .	. .	. .	. .	1	. .	. .	.
Cyphonautes sp.	. .	. .	. .	. .	2	20	. .	1	.
Actinia sp.	. .	. .	. .	. .	1	. .	. .	. .	.
(Amphioxus lanceolatus)	. .	. .	. .	. .	. .	. .	. .	2	.
Total number of specimens	22	392	342	213	94	364	40	173	1,1
Total number of species	6	8	7	7	8	9	9	15	
Total for the whole pump-series: 32 species. Total number of larvae in a water column covering 1 sq.m of bottom: 75,000.	The Baltic water contains: 21,000 larvae (= 28 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 21 species (i. e. on an average 8 species per 100 l water).							The Kattegat v contains: 54,000 vae (= 72 % c total larval stoc a water column c ing 1 sq.m of bo comprising 23 sp (i. e. on an avera species per100 l w

Pump-series taken off Ven, depth 0—17 m (bottom), on August 22nd, 1937. From each metre 100 l of water were pumped up (cf. the text on p. 383). Larvae with an * were caught dead.

0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
.5°	19.4°	19.4°	19.4°	19.4°	19.3°	19.3°	19.2°	19.2°	19.1°	18.5°	18.0°	16 5°	14.5°	11.7°	11.0°	10.4°	10.1°	
									(+)	(+)	(+)	+	+	+ +	+			
?	?	?	?	?	?	?	?	?	*Ceratium*	*Ceratium*	*Ceratium*	*Ceratium*	*Ceratium*	*Ceratium* *Peridinium*	*Ceratium*	?	?	
..	..	..	..	..	..	..	..	..	..	*3	..	..	..	*1	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	*1	..	*1	..	*1	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	1	3	2	..	1	7	4	1	2	..	1	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	1	..	3	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	2	2	..	1	..	..	
..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	
..	..	..	..	..	2	..	..	..	11	3	..	4	4	1	..	..	..	
..	..	..	..	..	..	..	..	..	..	20	6	8	2	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	3	24	4	..	2	4	..	..	
..	..	..	..	..	..	..	..	..	1	19	6	14	3	1	1	1	..	
..	..	..	..	..	..	..	..	..	..	..	..	1	4	3	2	1	2	
..	..	..	..	..	..	..	..	..	..	4	2	6	4	8	7	2	1	
..	..	..	..	..	..	..	..	..	1	..	..	1	..	2	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	1	4	1	..	..	
..	..	..	..	..	..	1	..	..	..	4	3	8	20	13	7	11	21	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	1	5	2	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	3	4	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	2	3	..	..	1	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	3	5	12	16	2	..	..	..	
..	..	..	1	3	3	3	..	..	12	75	16	54	64	67	7	6	6	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	1	..	5	23	1	..	..	3	3	
..	..	..	..	..	..	..	..	..	..	14	2	6	..	1	..	..	..	
..	..	..	..	..	..	..	..	..	..	4	..	2	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	10	11	6	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	
..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	1	..	..	
..	..	..	..	..	..	..	..	..	..	2	2	4	3	3	2	1	2	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	7	6	13	..	..	..	..	..	
0	0	0	1	4	8	6	0	1	33	179	90	173	139	120	36	25	37	Total number of specimens
0	0	0	1	2	3	3	0	1	6	17	14	21	18	19	13	7	8	Total number of species

The Baltic water contains: 500 larvae (= 7 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 7 species (i. e. on an average 2 species per 100 l water).

The Kattegat water contains: 7,200 larvae (= 93 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 33 species (i. e. 15 species per 100 l water).

Total for the whole pump-series: 33 species.

Total number of larvae in a water column covering 1 sq.m of bottom: 7,700.

	Pump-series taken off Ven, depth 0—19 m (bottom), on September 25th, 1 marked								
Depth in metres	0	1	2	3	4	5	6	7	8
Temperature (Centigrade)	14.7°	14.8°	14.8°	14.8°	14.7°	14.7°	14.7°	15.0°	15.
Estimate of the volume of Phytoplankton. ÷ = No Phytoplankton caught by the net, (+) = very poor	÷	÷	(+)	÷	÷	÷	÷	(+) *Ceratium*	(+ *Cerati*
Psammechinus miliaris	..	..	..	..	..	..	..	..	..
Echinocyamus pusillus	..	..	..	..	..	..	..	..	11
Brissopsis lyrifera	..	..	..	..	..	..	..	..	..
Ophiura albida	..	..	..	..	..	..	..	..	..
Amphiura filiformis	..	..	..	..	..	..	..	..	..
Littorina littorea	23	43	7	10	17	8	3	8	..
Alvania abyssicola	..	..	..	..	..	..	..	..	..
Bittium reticulatum	..	..	..	..	..	..	..	3	..
Odostomia sp.	..	..	..	..	..	..	..	..	..
Rissoa sp.	..	..	..	..	..	..	..	..	..
Coecum glabrum	..	..	..	..	..	..	..	..	..
Eulimella nitidissima	..	..	..	..	..	..	..	..	..
Natica montagui	..	..	..	..	..	1	..	..	..
Nassa reticulata	..	..	..	1	..	..	2	5	22
Prosobranchiata sp.	..	..	..	..	..	..	..	..	..
Philine aperta	..	1	..	..	..	..	..	..	..
Acera bullata	..	..	..	..	..	..	..	..	..
Retusa umbilicata	..	..	..	..	..	..	..	..	..
Limapontia capitata	..	..	..	..	..	..	..	2	..
Elysia or *Stiliger*	..	..	..	..	..	..	..	..	..
Anomia squamula	..	..	..	..	..	..	..	..	..
Mytilidae sp.	..	..	..	1	..	..	..	..	..
Cardium fasciatum	..	..	..	..	..	..	..	..	..
Tellina sp.?	..	..	..	..	..	..	..	..	1
Cultellus pellucidus	..	..	..	..	..	..	..	..	..
Montacuta bidentata	..	..	..	..	..	..	..	..	..
Venus gallina?	..	..	..	2	..	1	..	2	2
Lima loscombi	..	..	..	..	..	..	..	..	..
Saxicava arctica	..	..	..	..	..	..	1	..	..
Teredo navalis	..	..	..	..	..	..	..	..	..
Lamellibranchiata sp.	2	3	2	4	3	2	2 spp., 5	7	8
Polydora ciliata	..	..	..	1	..	..	..	..	..
Spionidae sp.	..	..	..	..	..	..	..	..	..
Magelona papillicornis	..	..	..	..	..	..	..	..	..
Spio filicornis	..	..	..	..	..	..	..	..	..
Phyllodoce groenlandica	..	..	..	..	..	..	..	..	..
Eteone sp.	..	..	..	..	..	..	..	..	..
Disoma multisetosum	..	..	..	..	..	..	..	..	..
Pectinaria koreni	..	..	..	..	..	..	..	..	..
Polychaeta sp.	..	..	1	..	..	..	..	..	..
Balanus, Nauplia	..	..	..	..	..	..	..	..	2
Cyphonautes sp.	..	..	..	..	..	..	..	..	1
Pilidium sp.	..	..	..	..	..	..	..	..	..
Total number of specimens	25	47	10	19	20	12	11	27	37
Total number of species	2	3	3	6	2	4	5	6	7
Total for the whole pump-series: 44 species. Total number of larvae in a water column covering 1 sq.m of bottom: 15,200.	The Baltic water contains: 1,700 larvae (= 11 °/₀ of the total larval stock) a water column covering 1 sq.m of bottom, comprising 17 species (i. e. on average 4 species per 100 l water).								

om each metre 100 l of water were pumped up (cf. the text on p. 383). Larvae marked with an * were caught dead. Figures (*) show that some of the larvae were caught dead.

9	10	11	12	13	14	15	16	17	18	19
14.9°	14.4°	13.9°	12.7°	12.3°	12.0°	11.9°	11.6°	10.8°	9.6°	9.4°
?	÷	(+) *Ceratium*	÷	÷	÷	÷	÷	÷	÷	÷
..	1	..	..	..	..	..	..	..	..	..
1	*1	2	*1	1	..	..	..	..	..	..
..	2	1	1	..	..	..	..	..	..	..
..	3	4	..	3	..	..	..	..	..	..
2	(*)27	(*)19	(*)3	(1)	1	..	1	..	..	..
3	..	1	..	..	..	..	..	..	..	..
..	3	1	2	1	..	..	..	..	..	..
1	..	..	..	..	..	..	..	..	..	..
..	..	..	..	1	..	..	..	..	..	..
..	..	..	1	..	..	..	..	..	..	..
..	..	1	1	..	..	.	..	..	..	..
..	..	1	2	1	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	.	..
73	48	30	26	6	1	2	..	..	..	..
..	1	..	12	..	..	..	1	..	..	..
4	22	45	24	7	7	3	..	4	..	..
..	1	4	1	1	2	..	1	..	..	..
1	..	3	2	..	4	1	1	..	..	..
..	2	1	1	2	..	..	1	..	..	..
..	..	..	..	2	..	..	..	..	..	..
1	3	1	4	2	..	..	..	..	1	..
3	8	2	10	4	3	1	1	3	..	..
1	3	4	2	2	..	1	1	..	..	..
1	2	4	4	2	5	1	..	..	..	..
1	3	3	50	60	3	1	..	..	..	..
..	7	10	32	15	1	2	..	..	..	..
1	8	..	2	2	1	4	..	..	..	..
..	..	1	4	..	..	..	..	..	..	..
..	5	1	3	..	..	..	..	..	..	..
..	..	..	+	2	1	.·.	..	..	..	1
57	175	85	135	75	13	2 spp., 7	6	1	1	..
..	..	..	..	1	1	7	6	1	1	..
..	..	..	..	1	..	1	3	1	2	..
..	..	..	1	..	..	1	..	..	..	..
2	..	..	..	..	..	..	..	..	..	..
..	..	..	1	..	..	..	..	..	..	..
..	1	..	..	1	..	..	..	..	..	..
..	..	..	2	..	..	..	..	..	..	..
..	1	..	..	..	..	1	..	..	..	..
..	..	..	2	1	1	..	..	1	..	..
..	..	..	..	..	..	..	1	1	..	..
5	10	6	5	..	..	..	..	..	..	..
..	1	..	..	..	..	..	..	1	..	..
157	338	230	334	193	44	23	17	11	4	1
16	24	23	28	23	14	14	10	6	3	1

he Kattegat water contains: 13,500 larvae (= 89 % of the total larval stock) in a water column covering 1 sq.m of bottom, comprising 43 species (i. e. on an average 15 species per 100 l water).

Philine aperta, Retusa umbilicata, Anomia squamula, Cultellus pellucidus, Cardium fasciatum, Montacuta ferruginosa, Pectinaria koreni, ?Disoma multisetosum, the *Cyphonautes*-larvae, and all the Echinoderm-larvae (101 out of the 103 living Echinoderm-larvae taken in our pump-series were found in the Kattegat layer!). All these larvae are frequent, but no single species of them will ever attain such high figures as were found for *Littorina littorea* or *Mytilus edulis* in the Baltic layer. The commonest species are probably *Nassa, Philine,* and *Cyphonautes.*

The results obtained from the series analysed above give, then, the following figures: Altogether 60 species of larvae were found in our pump-series. Of these, 33 species were represented in the Baltic water, 57 species in the Kattegat water; 30 species were common to both water layers; 3 species (*Natica montagui, Mya arenaria,* and a larval *Actinian*) were only found in Baltic water, and 27 species seem to occur exclusively in the Kattegat layer. The total number of larval specimens in our pump-series calculated for the water column over 1 sq.m of bottom is about 117,000. Of these, 29,000 (= 25 per cent) belong to the Baltic layer, and accordingly 88,000 (= 75 per cent) to the Kattegat layer.

If to these calculations we add our experiences from the 9 months from which no pump-series are at hand, we obtain the following facts: The month of June has a Baltic larval stock nearly just as large as that found in July, but except for the months June—July—August no large spawning is known from the Baltic water layer. The Kattegat spawning, however, though decreasing in November, will reach a new maximum in the number of specimens in (late November) December—January, when immense swarms of larval *Mya truncata* will dominate in the water masses. Ten vertical hauls taken on $^{24}/_{1}$-38 from each of the following water columns off Ven: 10—0 m, 15—0 m, and 18—0 m, contained: 740, 1260, and 1500 *Mya*-larvae respectively, which shows that the larvae in question are uniformly distributed throughout the whole water mass, a fact which is in good agreement with the lack of a distinct spring layer on these days (cf. table p. 381, on $^{23}/_{1}$-38). As the adult *Mya truncata* is mainly associated with the Kattegat water, it seems reasonable to assume that this layer has been totally dominating in the Sound on the days mentioned. Thus, when our experience from the remaining part of the year is included in the calculations from the pump-series, the characteristics shown by the latter are further intensified. In the northern and middle parts of the Sound the Kattegat larvae constitute the absolutely dominant element in the plankton in regard to species as well as to number, while the Baltic water layer, though covering the surface nearly throughout the year, has a rather small stock of larvae.

In the middle part of the Sound (off Ven) the Kattegat layer will probably contain at least 80 per cent of all the larvae occurring in the plankton. Our main-series show, however, that the number of larvae (per 10 vertical hauls) is nearly twice as large off Helsingor as off Ven, viz. 7,500 and 4,000 larvae respectively, and the calculations stated on pp. 376—379 seem to show that the stock of larvae in the Baltic layer is equally large or nearly equally large in both localities, i. e. the larger number of larvae off Helsingor must occur in the Kattegat layer. The percentage of larvae in the Kattegat layer will, accordingly, be still larger off Helsingor than off Ven, probably constituting more than 90 per cent of the total stock of planktonic larvae for the whole year. A large percentage of these larvae in the Kattegat layer originates, as mentioned on p. 378, from parents in the Kattegat.

These large numbers of larvae in the Kattegat layer are in good agreement with the rule of "concentration of the vertical region in the Sound" mentioned by various authors (cf. i. a. BRATTSTRÖM 1941, p. 260). This rule means that several adult invertebrates which live in the littoral zone in the North Sea and the Kattegat are forced by the brackish surface layer to submerge in the Sound, having their main occurrence here below the spring-layer, while other species, which in the Kattegat live at greater depths, rise to smaller depths in the Sound, although, of course, they will remain below the spring-layer. A species common at depths of 40 to 60 m in the Kattegat will find corresponding hydrographical conditions (i. a. low temperatures) in the Sound already at depths of 20 to 30 m and will accordingly ascend to these depths. The area of the Sound covered by Kattegat water has, therefore, an astonishingly great concentration of adult invertebrates, species as well as specimens — a fact which helps us to understand why such a great majority of larvae are associated with the Kattegat layer. However, a large number of the larvae occurring in this water layer are "drift-larvae", which have been carried to the Sound from the Kattegat (cf. pp. 378—379).

The pump-series from Ven were taken in those months of the year in which two of the largest maxima of larvae occur in the Sound. Accordingly, the number of larvae per main-series must be supposed to be much larger than the average amount of larvae for the whole year — a fact which is supported by the figures for the main-series. Each of the five pump-series contains on an average 23,500 larvae in a water column covering 1 sq.m of bottom. This average-number is probably estimated too high, as the series of 75,000 larvae from August was on purpose taken during a remarkably large, not normal, maximum of *Polydora* larvae. When this series is disregarded, the average number of larvae will be about 10,500. The minimum number of larvae over 1 sq.m of bottom in the pump-series is 7,000 and the maximum — as mentioned above — 75,000.

The present author has worked up the bottom animal larvae found in a number of quantitative plankton samples from the Isefjord (Bramsnæs Vig, collected by Dr. E. Steemann Nielsen). The samples were taken in 1941, and the larval contents in 8 l of surface water and 8 l of bottom water from each date was preserved (the area in question is 4 to 5 m deep). Owing to the very large contents of larvae these small volumes are sufficient for a calculation of the total number of larvae for the water column over 1 sq.m of bottom. The contents of larvae at the surface and near the bottom are almost the same, and interpolations between these figures form the basis of the calculations. From July—September, i. e. the same months during which pump-series were taken off Ven, 5 series are at hand from the Isefjord, which contained the following numbers of larvae:

July				August				September		Average number of larvae for the water column over 1 sq.m of bottom in July—September 1941
16th		30th		14th		27th		30th		
depth in m	number of larvae over 1 sq.m	depth	number	depth	number	depth	number	depth	number	
0	102,380	0	218,750	0	48,130	0	116,630	0	47,880	
4	77,880	4	63,250	4	32,750	4	139,000	4	87,750	
whole water column	360,000	whole water column	565,000	whole water column	162,000	whole water column	511,000	whole water column	271,000	375,000

The average number per water column, viz. 375,000 larvae, is thus 16 to 35 times as large as the corresponding averages from Ven, viz. 23,500 to 10,500 in the same months, and if the figures for the whole year are considered, it can be taken for granted that the Isefjord larvae will show a still more pronounced frequency as compared with the larvae in the Sound than is expressed by the above figures. While in the Sound the maximum spawnings of the year occur in the months July to September (cf. the curve fig. 198, p. 404), the maximum spawning in the Isefjord takes place already in the last days of May, when the larvae occur in a number of up to 16 millions over each sq.m of bottom. The largest figure from our pump-series from Ven, viz. 75,000 larvae, taken during an abnormally large maximum of larvae, is thus only $^1/_{200}$ of the figure from the Isefjord maximum, and the largest figure from a main-series in the Sound, viz. 66.000 larvae (off Helsingor on $^{11}/_{11}$-41) is only $^1/_{230}$ of the number from the Isefjord.

The number of larvae per water volume in the Sound is thus small as compared with the figures from the Isefjord, and this latter locality seems to show features characteristic of the closed shallow-watered areas of the Danish seas. The pump-series from the Sound have shown that the number of bottom animal larvae both as regards species and specimens is much larger in the Kattegat water than in the Baltic water, and the calculations given on pp. 378—379 seem to show that 50 per cent or probably more of the larvae in the northern and middle parts of the Sound are "drift-larvae" from the Kattegat. These "drift-larvae" are mainly older larvae — the last remnants of a spawning in the Kattegat, larvae which are nearly ready to metamorphose when they reach the Sound. The large "waste" of young planktonic larvae in this brood has thus to all appearance taken place outside the Sound, and the larval stock is much reduced before arriving there.

5. The Percentage of the different Larval Components in the Sound.

The material at hand allows us to compare the relative frequency of the pelagic larvae belonging to the dominant animal groups.

However, this comparison will be of a much greater value, if we know in broad features the percentage composition of the adult animal stock on the bottom within the area in question. C. G. Johs. Petersen (1911, table VI, No. III—VIII) gives the number of species per sq.m of level sea bottom for six localities in the northern and middle parts of the Sound (taken in 1910), viz.

Off Kullen	30—40 m,	10 stations,	50 samples
Off Höganäs	20—24 m,	10 —	50 —
Off Snekkersten	3— 4 m,	5 —	50 —
North of Ven	21—31 m,	10 —	50 —
South of Ven	14—16 m,	10 —	50 —
Lous Flak	9—11 m,	10 —	50 —

The contents of these 300 samples taken with the 0.1 sq.m Petersen-grab from localities equally distributed all over the northern and middle parts of the Sound seem to give a good and reliable picture of the relative frequency of the species belonging to the different animal groups of the level sea bottom. In order to use the samples for a comparison with the plankton series, only such species from Petersen's lists have been taken into con ideration as are known to have a pelagic larval development. Adding such species from the 300 samples, we shall find the following percentual frequency (number of specimens with pelagic larvae):

Lamellibranchs	36 %
Prosobranchs	4 %
Tectibranchs	1 %
Polychaetes	29 %
Echinoderms	30 %
	100 %

The number of specimens seems thus to be nearly the same for Lamellibranchs, Polychaetes, and Echinoderms on the level sea bottom, and 270 further bottom samples from 1911 taken in eight localities in different parts of the Sound (PETERSEN 1913, table pp. 51—53) give precisely the same result. However, the number of species in these latter samples is so often referred to as "fragments" or as "∞", that they cannot be used for a percentage calculation.

It is much more difficult to give the relative frequency within the epifauna, as no really quantitative data are available. An estimate based on several years' experience with dredge hauls and on the epifauna tables in PETERSEN (1918) gives the following results. The stock of Lamellibranchs, especially *Mytilus* and *Modiola*, constitute a still larger percentage than the Lamellibranchs on the level bottom. The number of Prosobranchs is much larger in the epifauna, e. g. *Littorina littorea*, *Lacuna divaricata*, and partly *Nassa reticulata*, the latter also living on the level bottom. The larvae of *Hydrobia* and *Rissoa* are of little importance in the plankton of the open sea. The number of Polychaetes is also fairly great, especially that of *Polydora*, while Serpulids, Cirratulids, and most Terebellids have a non-pelagic development or a much shortened pelagic life. The number of Echinoderms is rather large (*Asterias*, *Echinocyamus*, *Psammechinus*, *Strongylocentrotus*, *Ophiopholis*, *Ophiothrix* etc.), though somewhat smaller than on the level bottom. Further, Bryozoans (especially *Membranipora*) are very common here.

In the Sound, however, the fauna of the level bottom seems to be somewhat more important than the epifauna, the former occupying the larger areas. The percentages found from PETERSEN's samples, influenced by the percentages found for the epifauna will, therefore, imply rather small corrections of the level bottom figures given above. Only for the Prosobranchs will the figures be essentially altered.

Hence, if the percentages for the level bottom animals as well as the epifauna animals with pelagic larvae of all the animal communities occurring in the northern and middle parts of the Sound are estimated, the following percentages would seem to reflect the real conditions fairly well:

Lamellibranchs	40 %
Prosobranchs	10 %
Tectibranchs	0.5 %
Polychaetes	20—25 %
Echinoderms	20—25 %
Bryozoans	3.5 %

As these figures refer exclusively to species which have a pelagic larval stage, it might be expected that the stock of larvae in the plankton would be distributed roughly on a similar scale within the different groups as stated for the adults. Among the species with pelagic larvae, however, the Lamellibranchs exhibit eggs between 50 and 100 μ in diameter (average 72 μ), the Prosobranchs 60 to 320 μ (average 155 μ), the Polychaetes 62—180 μ

(average 120 μ), and the Echinoderms 100—185 μ (average 135 μ). The three last-mentioned groups have, thus, eggs of nearly the same size, while the eggs of the Lamellibranchs are much smaller. Accordingly a larger number of eggs will probably be produced by a single specimen within the Lamellibranchs than within the other groups. The number of eggs shed by a single Prosobranch or Polychaete specimen is only poorly known, but it is known that the number of eggs produced by a single *Littorina littorea* (several spawnings of about 500 eggs each per month) and *Nassa reticulata*, which are dominants, is fairly large and the number of eggs laid by a single *Polydora ciliata* (the absolute dominant among the Polychaetes) is rather small, viz. about 400 per batch (Wilson 1928 a). Within the Echinoderms, the Ophiurans have only rather small amounts of eggs, estimated by Dr. Mortensen (verbal information) at a few thousands, while the eggs of a single regular Echinid may amount to hundreds of thousands.

This forms a basis for the conjecture that the larvae of Lamellibranchs and Prosobranchs will occur in the plankton in a somewhat larger number than might be expected judging from the frequency of the parents, while the Polychaete larvae will be somewhat less common, and the Echinoderm larvae about as common as might be expected from their frequency in the adult stage.

The below table shows the percentage of larvae based upon the main-series from Ven and Helsingør:

Animal group	Ven (45 main-series)	Helsingør (20 main-series)	Total % af all main-series from Ven and Helsingør
Echinoderms	0.8 %	3.2 %	1.9 %
Polychaetes	15.1 %	6.0 %	10.9 %
Prosobranchs	14.7 %	9.9 %	12.5 %
Tectibranchs	1.8 %	1.6 %	1.7 %
Ascoglossids	0.2 %	2.5 %	1.3 %
Nudibranchs	0.4 %	1.1 %	0.7 %
Lamellibranchs	62.9 %	50.7 %	57.3 %
Decapods	0.0 %	0.1 %	0.1 %
Cyphonautes	3.5 %	24.1 %	12.9 %
Balanids	0.5 %	0.7 %	0.6 %
Other larvae	0.1 %	0.1 %	0.1 %
Total...	100.0 %	100.0 %	100.0 %

The number of larval Lamellibranchs is very large—perhaps somewhat larger than expected—in both localities, constituting more than half of all the larvae occurring in the plankton. Accordingly the percentages of the other groups will be somewhat reduced. The Prosobranchs, however, have a larval percentage agreeing very well with that calculated from the stock on the bottom. The Polychaetes are less numerous in the larval stage than calculated, probably owing to the total dominance of the *Polydora*-larvae, of which — as mentioned above — the individual adult female produces only a fairly small number of eggs. The Echinoderms, finally, the fourth of the large animal groups dominating the bottom, show a very surprising picture when compared with the number of parents in the Sound. The larvae were calculated to represent 20—25 per cent of all the bottom animal larvae, and the figure really found is only

1.9 per cent (0.8 % off Ven, and 3.2 % off Helsingør). This seems even more peculiar when compared with the characteristics of the adults given by Petersen (1911, p. 55), viz. "In the Northern part of the Sound and W.N.W. of Kullen we investigated 3 localities in deep water (table VI); they show a quantity of echinoderms whose alcohol weight is approximately equal to or more than half of the total animal life," and ". . . . there is no doubt that echinoderms both in volume and weight are exceedingly abundant at many localities in the deep Kattegat, in the Belt Sea at Samsø and in the northern and deep parts of the Sound."

The very pronounced dominance of larval Lamellibranchs may i. a. be explained by the fact that these larvae have a very rapid development in their first stages. Their veliger larvae occur in the plankton already from 12 to 48 hours or even earlier after the eggs have been fertilised. Thus in addition to the stock of older larvae carried to the Sound from the Kattegat, the whole stock of larvae produced within the Sound itself will be present in the plankton as recognisable larvae already before the water masses have left the Sound (cf. p. 425). The Prosobranchs have a similar advantage, as most of their larvae spend a week or so within an egg capsule, commencing the planktonic life as fully developed Veligers. The same is the case with the commonest Polychaetes, thus the genus *Polydora* and several other Polychaetes. The Echinoderms, however, although their eggs are shed freely in the water, will often take about 6—7 days before the eggs are so differentiated that the larvae are recognisable as Echinoderms on a rapid examination.

While several of the dominant species of larvae within the Lamellibranchs (*Mytilus edulis, Mya arenaria, Cardium edule, Macoma baltica*) and the Prosobranchs (*Littorina littorea, Bittium reticulatum* etc.) are closely associated with the Baltic layer, nearly all the Echinoderm-larvae in the Sound are exclusively associated with the Kattegat layer. Larvae belonging to the Kattegat layer (high salinity) will perish rather quickly when transferred to Baltic water (low salinity, brackish). Several experiments have shown, however, that larvae associated with the Baltic layer will thrive well when transferred to Kattegat water. As regards our main-series the larvae from all the vertical hauls were usually taken to the laboratory in Kattegat water, where the whole stock thrived well. If transported in Baltic water, however, a large part of the larvae, especially the Echinoderms and the Polychaetes, were dead on arrival to the laboratory. Mixtures of the two layers accordingly present no danger to the larvae in the Baltic layer, but will be very critical to the larvae of the Kattegat layer. The Kattegat layer, flowing southwards in the Sound along the bottom and storing up all larvae shed in the deeper parts of this area, on reaching the "threshold Amager—Limhamn" or even earlier (cf. pp. 23—25) will be forced towards the surface and mixed with Baltic water, where large parts of its contents of larvae will perish. Hence, among the stock of larvae produced in the Sound itself the risk of being destroyed is much larger for the larvae of the Echinoderms and certain young Polychaetes than for the larvae of the other groups.

Further, the Echinoderm-larvae are much better fit for a passive transport in the water masses than the larvae of the other groups. Larvae e. g. of Polychaetes are able to swim very actively about (e. g. *Magelona, Poecilochaetus, Polydora*), and even larval Prosobranchs and Lamellibranchs in proportion to their volume have a much more active locomotion than those of the Echinoderms. Such a locomotion, especially in a vertical direction (away from the brackish water layer), will, no doubt, be of some significance. Besides, the Echinoderm-larvae seem to be very sensitive. Together with certain young Polychaete-*Trochophora's* they are the first larvae to die in our samples, and their whole soft surface is exposed to the surrounding water masses, while the larvae of the Lamellibranchs and Prosobranchs are protected by their shells. Apart from the direct protection, these shells have also another advantage. When swimming larvae of Lamellibranchs or Prosobranchs are disturbed, they will at once withdraw their velum into their shells and sink to the bottom.

If, now, a larval Lamellibranch or Prosobranch belonging to the Kattegat layer is forced to the surface by the "threshold" mentioned above, it will be exposed to the Baltic water and will be carried northwards through the Sound with this current. The brackish water, however, will be unpleasant to the larva, which will immediately withdraw into its shell, thus avoiding, at least for some time, the influence exerted by the Baltic water. On withdrawing, the larva will begin to sink to the bottom and will have a good chance of reaching the deeper-lying Kattegat water a few hours to a few days later. The Echinoderm larvae, however, have no mechanism which allows them to sink to the bottom. They float passively about totally exposed to the brackish water, and will accordingly perish in large numbers.

The small percentage of Echinoderm-larvae, further, comprises a large number of older larvae, i. e. larvae originating from the Kattegat, and often the majority of these larvae are already provided with a young bottom stage inside, thus being nearly ready to metamorphose and like all late larvae they are more resistant to unfavourable conditions than the early larval stages (cf. p. 423). This small stock of Echinoderm-larvae from the Kattegat should probably be regarded as the few laggards of a larval stock spawned in the Kattegat, the largest number of which have completed their metamorphosis and left the plankton before arriving in the Sound. The laggards which actually reach the Sound will settle very soon with a rather small "waste" of larvae, as this "waste" has taken place already during their development in the Kattegat. In spite of their small percentage in the Sound, they will therefore be sufficiently effective for recruiting the stock on the bottom (cf. p. 363).

The surprising fact that larvae of epifauna forms are more numerous in the plankton than larvae of infauna forms (cf. pp. 396—398), may probably also contribute to explain the disagreements between the frequency-percentage of the different groups of the adult invertebrates (with a pelagic development) on the bottom and the larvae of the same groups in the plankton. From the maps (cf. Petersen 1918) it seems evident that the level bottom areas (infauna) comprise larger parts of the bottom in the Sound than the epifauna areas, while in spite of this the plankton shows a dominance of epifauna larvae (cf. below).

6. Epifauna Larvae as compared with Level Bottom Larvae.

The main-station off Ven, situated in the central part of the Sound, is surrounded by an area of rather large mud flats at a depth of 10—20 m and has a fairly weak current. The distance to the Kattegat is rather great and the water is too shallow here to allow the deepest part of the Kattegat-water to enter these areas regularly. The main-station off Helsingør is situated in the northern part of the Sound, in an area with a very strong current (up to 3—4 knots), with large sandy areas and — at greater depths — hard clay and soft mud. Stone-reefs and shell-banks are common at all depths down to 30 m; southern Kattegat is not far away, and the large depths of the area (up to 40 m) allows the Kattegat water to enter.

Considering the northern and middle parts of the Sound, it seems reasonable to expect that larvae of parents from the level bottom areas will dominate in our main-series, and that these level bottom larvae will be more numerous off Ven than off Helsingør; however, the calculations from the main-series given below seem to show that the epifauna-larvae preponderate in number in both localities.

Such calculations, however, include one source of error, viz. that all the larvae which still remain unidentified as to species cannot be referred to their right ecological substratum. Further, for a couple of well identified larvae it has also been impossible to decide whether their parents are most closely associated with the infauna or with the epifauna. Such larvae are those of *Pecten opercularis, Pecten septemradiatus, Nereis diversicolor*, and *Nereis pelagica*. If these latter larvae, and especially the several unidentified larvae, could have been taken into consideration, the results arrived at would probably have been somewhat different, although hardly to such a degree that the main result would have been different.

To the epifauna element the larvae of the following genera and species have been referred:

Echinodermata: *Asterias, Ophiothrix, Ophiocomina, Psammechinus, Echinus, Strongylocentrotus, Echinocyamus*, and *Psolus*.
Polychaeta: All the *Polynoidae, Genetyllis, Phyllodoce, Eteone, Nerine*, and *Polydora ciliata*.
Prosobranchiata: *Acmaea, Lacuna, Littorina, Alvania, Rissoa, Bittium, Odostomia, Trophon, Velutina, Nassa pygmaea*, and *Bela trevelyana*.
Tectibranchiata: *Acera bullata* (partially belonging to the level bottom also).
Ascoglossa: *Limapontia capitata*, and "*Elysia* or *Stiliger*".
Nudibranchiata: All species found.
Lamellibranchiata: *Anomia, Pecten striatus*, all *Mytilidae, Saxicava, Zirphaea*, and *Teredo*.
Cyphonautes: All species found.
Crustacea: All the larvae of *Balanus*, and most larvae of the *Decapoda*.
Other larvae: *Phoronis* and *Actinia*.

To the infauna-element have been referred:

Echinodermata: *Astropecten, Amphiura, Ophiura robusta, Ophiura albida, Spatangus, Echinocardium*, and *Brissopsis*.
Polychaeta: *Nephthys, Glycera*, all the *Spionidae* apart from *Polydora ciliata*, but including *Polydora coeca, Magelona, Poecilochaetus, Disoma, Chaetopterus, Capitella, Owenia, Myriochele, Pectinaria*, and *Artacama*.
Prosobranchiata: *Onoba, Coecum, Eulima, Eulimella, Aporrhais, Natica*, and *Nassa reticulata*.
Tectibranchiata: *Actaeon, Retusa, Diaphana, Philine*.
Ascoglossa: None.
Nudibranchiata: None.
Lamellibranchiata: *Lima loscombi, Montacuta, Cardium, Venus, Cultellus, Macoma, Tellina*, and *Mya*.
Cyphonautes: None.
Crustacea: *Crangon, Pandalus, Palaemon, Pandalina*.
Other larvae: *Pilidium*.

When the larvae are grouped according to the above scheme, the calculations will show the following results:

Locality	Ven, sum total from 45 main-series		Helsingør, sum total from 20 main-series	
Ecological type	Epifauna	Infauna	Epifauna	Infauna
Echinodermata	205	1,223	311	4,438
Polychaeta	8,837	15,006	1,702	5,558
Prosobranchiata	23,292	1,600	10,535	3,533
Tectibranchiata	804	2,330	322	2,067
Ascoglossa	393	0	3,751	0
Nudibranchiata	707	0	1,673	0
Lamellibranchiata	15,338	7,527	21,533	36,568
Cyphonautes	6,173	0	36,000	0
Crustacea	1,013	0	1,200	102
Other larvae	48	22	28	6
Total number of specimens...	56,810 = 67 %	27,708 = 33 %	77,055 = 59 %	52,272 = 41 %
Total number of species...	about 50	about 55	about 55	about 60

These figures, which must be treated with caution and only in very broad features, show that the specimens of larvae belonging to epifaunal forms are somewhat more numerous than those belonging to infauna forms, while the number of larval species are nearly identical within the two types of biotopes with a small surplus to the infauna-larvae. Within the Echinoderms, Polychaetes, and Tectibranchs, the infauna element dominates among the larvae. The Lamellibranch-larvae are recruited to nearly the same extent from the infauna and the epifauna with a slight dominance of infauna-larvae, while the larval Prosobranchs and Crustaceans (especially the *Balanus*-larvae) are rather closely associated with the epifauna forms. Finally, the larvae of Ascoglossids, Nudibranchs, and Bryozoans, are exclusively associated with the epifauna.

7. The Number of Larval Species in the different Months of the Year.

The total number of planktonic larvae of bottom invertebrates known from the Sound and taken in our main-series from Ven and Helsingør amounts to about 160 species, viz.

Echinoderms	16
Polychaetes	41
Prosobranchs	34
Opisthobranchs	15
Lamellibranchs	28—33
Decapods	12
Other larvae	13
about...	159—164,

of which by far the largest number is associated with the Kattegat layer (cf. p. 390). During the years of investigation off Ven 121 species of larvae were distinguished, and during the investigations off Helsingor we were able to distinguish and recognise 138 species of larvae. The table on p. 399 and the graph shown in fig. 196 give the number of larval species in the different months of the year based upon all our main series and supplemental series from Ven and from Helsingør:

Ven. Number of species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Echinoderms	2	0	1	5	2	5	8	8	11	11	4	3
Polychaetes	14	6	17	19	14	15	19	21	15	14	8	12
Prosobranchs	9	1	3	7	6	10	11	17	15	12	5	8
Tectibranchs & Ascoglossids	4	1	2	2	6	6	5	7	6	9	4	5
Nudibranchs	2	1	2	3	1	2	1	1	1	1	1	3
Lamellibranchs	10	4	5	9	8	11	16	16	15	13	9	10
Decapods	0	0	1	1	4	1	3	5	1	1	0	0
Other larvae	5	3	6	6	5	3	5	6	5	6	6	5
Total for Ven	46	16	37	52	46	53	68	81	69	67	37	46

Helsingør. Number of species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Echinoderms	0	0	0	4	2	3	4	5	7	8	3	2
Polychaetes	10	10	9	16	18	15	15	10	17	15	7	13
Prosobranchs	4	1	0	8	5	10	14	11	18	15	7	5
Tectibranchs & Ascoglossids	4	1	1	2	4	6	6	7	5	7	4	3
Nudibranchs	2	1	1	2	1	3	2	2	3	2	2	3
Lamellibranchs	15	7	4	6	3	10	20	14	24	24	18	13
Decapods	0	0	1	2	4	4	6	2	7	3	1	0
Other larvae	4	5	2	4	4	6	3	5	6	9	7	7
Total for Helsingør	39	25	18	44	41	57	70	56	87	83	49	46

Total number of species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Echinoderms	2	0	1	6	3	5	8	9	11	12	4	4
Polychaetes	18	12	18	22	20	20	20	23	24	21	12	16
Prosobranchs	9	1	3	9	9	13	16	20	20	18	8	10
Tectibranchs & Ascoglossids	6	2	2	2	6	6	7	7	6	10	4	5
Nudibranchs	2	1	2	3	1	3	2	2	2	2	2	3
Lamellibranchs	18	8	8	12	9	14	24	21	26	24	19	17
Decapods	0	0	1	2	4	4	6	5	7	4	0	0
Other larvae	5	5	6	6	5	6	5	8	7	10	7	8
Total for the northern and middle parts of the Sound	60	29	41	62	57	71	88	95	103	101	56	63

The minimum number in the Sound is found in February, when the last larvae from the "Kattegat-spawning" have disappeared. The Echinoderms and Prosobranchs are then of no or little importance while the Polychaetes and Lamellibranchs are dominants. The same tendency is seen in March and in April, when the number of species is increasing, being twice that in February. The following months show a rather uniform increase in the number of species within all the groups, which continues steadily towards the maximum in June—July, when the "Baltic-spawning" is at its height. The pump-series (pp. 381—392), however, have

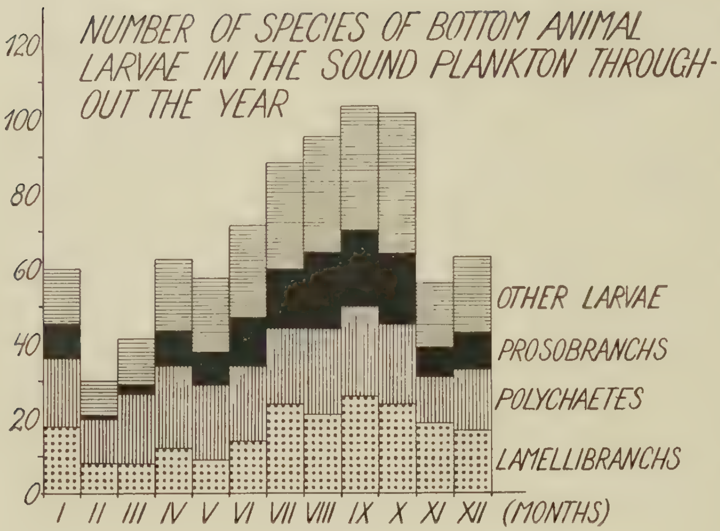


Fig. 196. Cf. the text on pp. 398—400.

shown that also the "Kattegat-spawning" has commenced, although it proceeds rather slowly during these months, to increase in August simultaneously with a decrease in the "Baltic-spawning". A few larvae belonging to the Baltic water may nevertheless occur in the autumn as late as November (and exceptionally as late as January), but the dominant element in September and October is found among the larvae in the Kattegat layer. Thus it might be expected that the maximum number of larval species for a single month would occur in September, when laggards from the Baltic spawning are still present, while the Kattegat spawning is in full progress. During this month the maximum in the number of species (viz. 103 species, i. e. $^2/_3$ of all the larval species known from the Sound) is reached as to nearly all the larger groups, viz. Echinoderms, Polychaetes, Prosobranchs, and Lamellibranchs, and a quite similar tendency and a similar number of species is characteristic of October. Subsequently the number of species decreases remarkably during November, December, and January to reach an absolute minimum in February.

8. The Spawning Seasons in the Sound.

The length of the spawning period in the Sound varies considerably from species to species. Judging from the occurrence of the larvae in the plankton we find for instance a fairly short spawning season, viz. 2—3 months, for: *Asterias rubens, Ophiocomina nigra, Psolus phantapus, Magelona papillicornis, Poecilochaetus serpens, Artacama proboscidea, Myriochele danielsseni, Natica montagui, Coecum glabrum,* and *Lima loscombi,* and a long spawning season, viz. 8—9 months, for: *Aporrhais pes pelecani, Bittium reticulatum, Nassa reticulata, Acera bullata,* and *Philine aperta.* Other species, finally, e. g. *Capitella capitata, Limapontia capitata, Zirphaea crispata,* and certain species of *Cyphonautes* and Nudibranchs seem to spawn in all months of the year, though with more or less pronounced maxima and minima. To this group may also be referred several species of Prosobranchs with a non-pelagic development such as: *Buccinum undatum, Neptunea antiqua, Nucella lapillus, Littorina saxatilis,* and *Hydrobia jenkinsi.* — However, by far the largest number of the species with pelagic larvae seem to spawn during a period of 5—6 months with a main-spawning during 2 or 3 months, and their spawning seasons seem to set in very regularly from year to year, some of them early and others late in the year according to the surrounding ecological conditions.

The poorest time in the plankton is February to March (as to the following remarks cf. the table on p. 403, fig. 197). In these months the number of larval species in the plankton ranges from 30—40 (in July to October from 90—100), and the number of specimens per main-series ranges from 2,200—3,500 (June: 5,600, July: 10,500, and August 5,000). The autumn spawning is over, and only a few late larvae of *Mya truncata* and *Nephthys ciliata* (the two latest breeding species of the autumn spawning) are still present in the plankton together with larvae of *Glycera alba* and *Nerine foliosa*, which seem to have their not very pronounced maxima in the unproductive part of the year. However, the main elements dominating during these months are the larvae of *Polydora*, especially those of *P. coeca*, which in February and March occur spontaneously in large numbers in the plankton. Their special mode of feeding (cf. pp. 446—447) render them independent of such food conditions as exclude other larvae at this time of the year. The larvae of *P. coeca* are still rather numerous, though decreasing in number, in April, May, and June, while those of *P. ciliata* reach their maximum in May. As the adult *Polydora* are met with at all depths from the shore to 30—40 m, it is impossible to illustrate their larval occurrence in the table on p. 403. A few larval Nudibranchs and some *Cyphonautes*-larvae are also found. To these may be added a number of species with a non-pelagic development. The spawning seasons of the star-fish *Henricia sanguinolenta* and *Asterias mülleri* are unknown from the Sound, but the literature reports that brood-protection is found in both of them off Norway and Scotland during the actual winter time. Also *Buccinum* and *Neptunea*, *Littorina saxatilis* and *Hydrobia jenkinsi* spawn in February and March as well as in any other month of the year.

Conditions in the spring. In April and May conditions will change, and the first indications of a new spawning can be observed. The new stock of larvae in the plankton originates from two quite different groups of adults, viz. adults associated with extremely deep water: *Ophiura robusta*, *Phyllodoce groenlandica*, *Myriochele danielsseni*, *Artacama proboscidea*, and *Aporrhais pes pelecani*, and adults associated with small depths (the Baltic surface layer), viz. *Cardium edule*, *Macoma baltica*, *Lacuna divaricata*, *Nereis diversicolor*, and the first few larvae of *Littorina littorea*, *Mytilus edulis*, and *Asterias rubens*. These two groups of larvae, those from the deep water and those from the shallow water, according to the figures from our main-series, seem to be nearly equally numerous in the plankton.

The deep water larvae originate from parents mainly living at greater depths than 20 m. The minimum temperature at a depth of 20 m in the northern and middle parts of the Sound is reached in March (mean temperature 4.8° C.), or even later at still greater depths. During April and May the 20 m temperature will increase to 5.3° C. and 6.1° C. respectively (Brattström 1941, p. 92, and this paper pp. 23—25). This slight rise of the temperature over the minimum of the year seems thus to be sufficient to induce spawning in a few species, while the majority of species of invertebrates living at these depths will spawn when the maximum temperatures (10°—12.5° C.) are reached in September to November, i. e. at just the opposite time of the year.

In April, when the first small spawning sets in, the shallow water larvae, the parents of which have their main occurrence within the Baltic surface layer, live at temperatures (average 3.5° to 4.5° C.) lower than those found at depths of 20 m during the same month. However, the temperatures found in the Baltic layer have already been considerably increased from the minimum in February (average 1.6° C.) and the daily temperature-amplitude is much greater in the surface layer than in the deeper water. Thus, already in April on calm and sunny days in sheltered, shallow-watered areas the temperature at the surface may rise considerably over the mean-temperature. Most of the larvae of the shallow water forms found in the plankton in April and May should, therefore, be regarded as the first forerunners of the regular summer-spawning, which sets in in real earnest in June.

Besides the forms with pelagic larvae there are also a few species with a non-pelagic development which are known to spawn at this time of the year. On the hard sand bottom off Hellebæk, depth 9—10 m, egg-balloons of *Scoloplos armiger* were taken in April, but were absolutely absent already in June. Similar egg-balloons are known from the Limfjord in May, and — according to the literature — along the North Sea coasts from (February) March to May. — Willemoës-Suhm (1871) found in the Bay of Kiel that the breeding-season of *Terebellides stromi*, two to three weeks, is in May. Finally, an egg string with non-pelagic developing larvae belonging to *Modiolaria discors* (a typical "*Zostera*-Lamellibranch") is recorded from Holbæk Fjord in May (Thorson 1935 b). As these two species also occur in the Baltic layer in the Sound (*Terebellides* also in deeper water), it seems reasonable to assume that, like *Scoloplos*, they are induced to spawn by the first small rise of the temperature in the surface layers.

The summer-spawning (= "the Baltic spawning"): The increase in temperature in the surface layer is very considerable during the spring. The average temperatures at the surface in April are 3.5° to 4.5° C., and for June 12.5° to 13.5° C., and in agreement with this the summer-spawning sets actively in early in June. At the same time the deep-water spawning declines slowly, the larvae of *Ophiura robusta* and *Polydora* being the last laggards, and in June and the beginning of July the shallow water larvae are predominant in the plankton. But as regards the shallow water larvae, also, conditions are now different from those prevailing in April to May, when *Nereis diversicolor, Lacuna divaricata*, and *Macoma baltica* were the dominants among the first outposts of the summer-spawning. These larvae are still rather frequent in June and July or even later, but the main spawning is especially characterised by the immense numbers of larvae of *Littorina littorea* and *Mytilus edulis*. However, also the larvae of *Cardium edule* and *Mya arenaria* are of common occurrence, and larvae of *Asterias rubens, Pygospio elegans*, and *Balanus* are characteristic "accompanying species" in the summer-spawning. *Pectinaria koreni*, which occurs very frequently in the hard sandy bottom at depths of 10—12 m in the northern part of the Sound, must be referred to the laggards of this spawning. In years with a normal growth of *Zostera* the larvae of Rissoids, first of all those of *Rissoa membranacea*, may also contribute to this maximum, though nearly all of these larvae develop swimming among the *Zostera*-leaves in quite shallow water. To this number may be added some species with a very short larval life, e. g. *Hydrobia ulvae* and *Spirorbis borealis*, or without any pelagic life at all, viz. *Littorina obtusata*. These three species are shallow-water inhabitants and typical summer-spawners, which reach the height of their breeding in June to July. — Only one of the common shallow-water forms is known to have a breeding season quite different from all the others, viz. *Arenicola marina*, which seems to spawn in the late autumn (cf. p. 109).

	June			July		
Locality / Larval type	Ven, average of 4 main-series	Helsingør, average of 2 main-series	Total for both localities	Ven, average of 4 main-series	Helsingør, average of 3 main-series	Total for both localities
Larvae of shallow-water species spawning in the surface layer	2,481 = 86 %	2,043 = 69 %	78 %	4,116 = 87 %	6,162 = 75 %	80 %
Larvae of species living in the intermediate zone..........	248 = 9 %	293 = 10 %	9 %	344 = 7 %	1,773 = 22 %	16 %
Larvae of species living in the bottom layer (Kattegat water)	135 = 5 %	614 = 21 %	13 %	266 = 6 %	263 = 3 %	4 %

In the two ice-free years (September 1937—September 1939) the spawning period seems to have set in two to three weeks earlier than after very strong ice-winters, e. g. 1942. On the other hand it would seem as if the spawning was more spontaneous in 1942, as if a larger number of specimens spawned as soon as the temperature was high enough.

In June and the first half of July the summer-spawning is at its height. The table p. 402, based on the main-series from Ven and Helsingor taken in June and July, shows the average

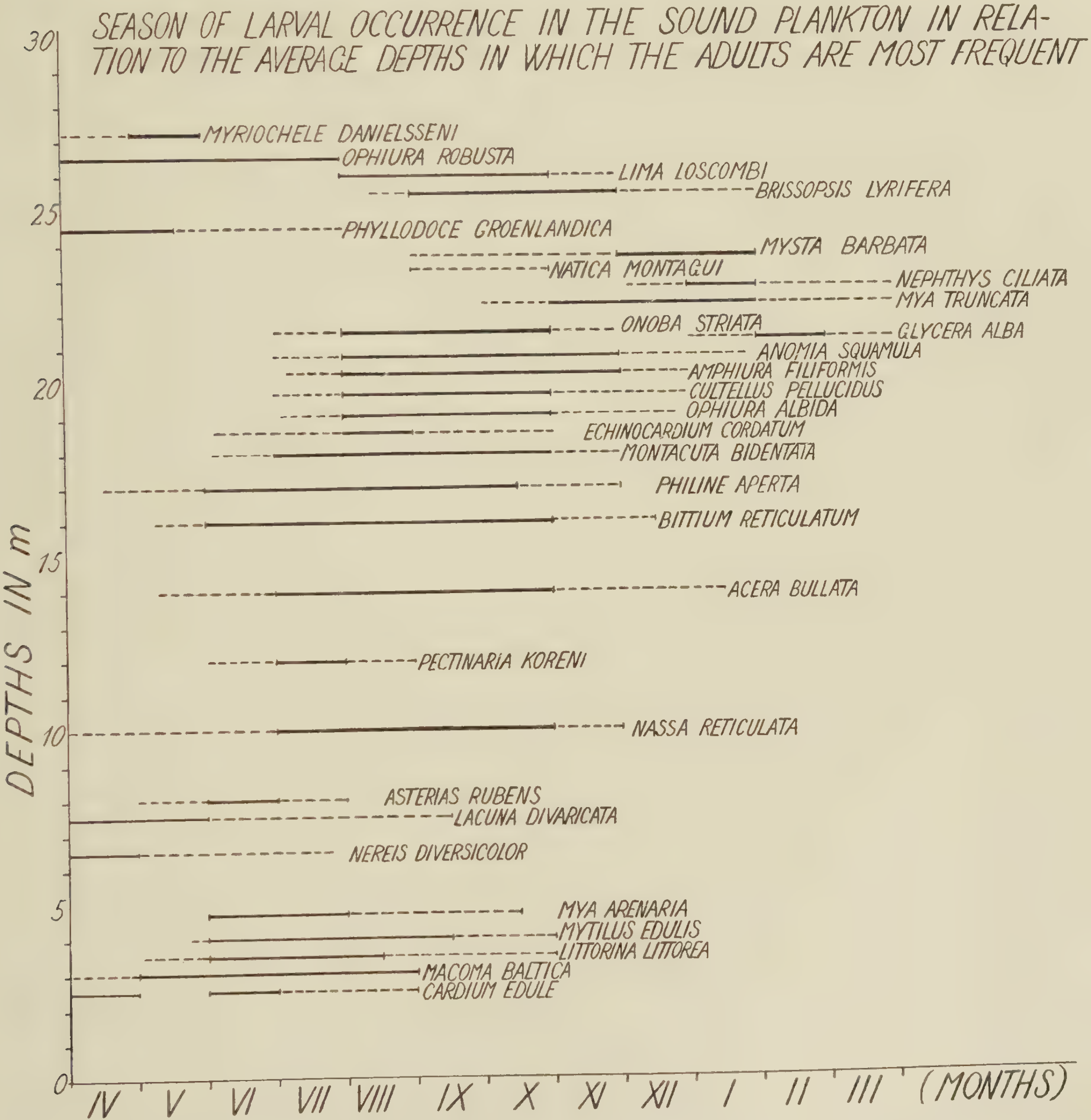


Fig. 197. Table showing the seasons of larval occurrence in the Sound (continuous lines = main occurrence, broken lines = scattered specimens) in relation to the depths at which the adults have their main occurrence. (Cf. the text pp. 400—408).

number of larval specimens per main-series and their percentage distribution in relation to the depths at which the parents live.

It will be seen that shallow water larvae preponderate in number in both months and in both localities, although they are less numerous off Helsingør than off Ven, constituting in June 78 $^0/_0$ and in July 80 $^0/_0$ of all the larvae in the plankton. This is all the more interesting since the number of larval species belonging to parents at intermediate and larger depths are more than twice (about 40 species) that found for the number of larval species with shallow water parents (17 species). Thus, the summer-spawning is poor in species, but rich in specimens. The larvae of *Littorina littorea* and *Mytilus edulis* alone constitute 76 $^0/_0$ (Ven, in June), 50 $^0/_0$ (Helsingør, in June), 79 $^0/_0$ (Ven, in July), and 67 $^0/_0$ (Helsingør, in July) respectively, i. e. half or more of all the larvae found in the plankton at this time of the year. The average numbers for July, however, are influenced by the large numbers of shallow water larvae during the first three weeks of the month. During the last week of July the deeper-living species show the first indications of spawning, and although the shallow water larvae are still frequently met with, the deep-water larvae will soon dominate in the plankton. This is seen very clearly from the pump-series taken off Ven in the last days of July, viz. on $^{27}/_{7}$-1937 and on $^{30}/_{7}$-1938, in which the shallow water larvae (i. e. the summer-spawning) constitutes only 34 and 20 per cent respectively of the total amount of larvae in the whole water column (cf. pp. 383—385). In a summer following upon a heavy ice-winter (e. g. 1942) the whole spawning-rhytm seems to take place two to three weeks later, and the dominance of the larvae of deep water species will be observed about the middle of August and not in July.

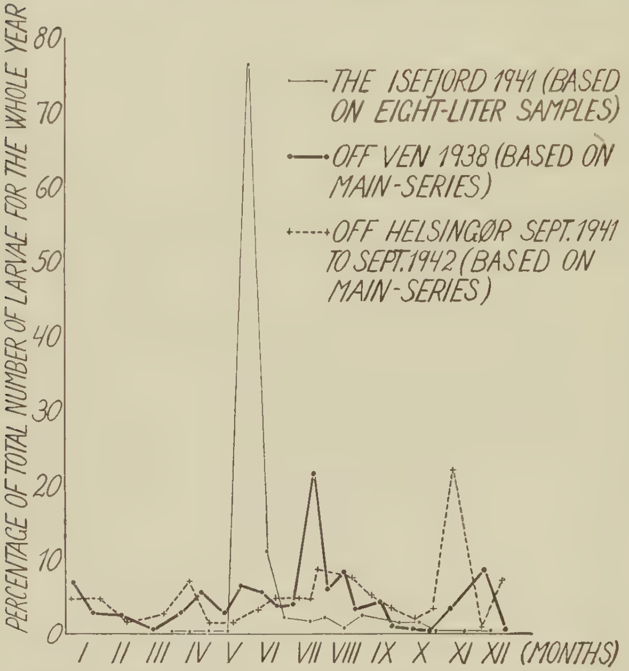


Fig. 198, showing the percentage distribution of the bottom animal larvae in the plankton throughout the year in the Sound off Ven and Helsingør, and in the Isefjord (cf. the text on pp. 404—405).

The summer-spawning occurs rather late in the Sound — a fact which can probably be ascribed to the considerable current and water movements, which retard the heating of the water. In the Danish fjords, with their shallow-watered areas, the large increase in the temperature takes place somewhat earlier in the year, and so does also the summer-spawning. The graphs in fig. 198 show the spawning conditions in the Isefjord and in the Sound off Ven and Helsingør, each point showing the percentage of the whole larval stock from all the samples taken during the year on a particular date in the particular locality. The summer-spawning, which in the Isefjord is the only spawning of any importance during the year, here sets in with a surprising intensity in the last days of May, reaching its maximum in a few days. Decreasing very rapidly, these large numbers of larvae have already disappeared from the plankton at the end of June, and only a relatively small stock of laggards is present until the end of

October. Later in the year, in winter and early spring, the larvae are nearly totally absent from the plankton in the Isefjord.

In the Sound the summer-spawning, although very distinct, is not by far so pronounced as in the Isefjord. It has been shown that the first few larvae in the Sound appear already in April—May, the spawning thus being much less spontaneous than in the Isefjord. The post-spawning has also a much wider range in the Sound. As late as August the larvae of *Mytilus* and *Littorina* are common in the plankton; they are still found commonly, though not very frequently, in September—October, and a few larvae may be seen as late as December and January.

Spawning of species living at intermediate depths in the Sound. Some of the species of bottom invertebrates in the Sound are so eurythermic and euryhaline that they are able to inhabit the zone from a depth of about (8) 10 to 16 (18) m — an area, which, varying with the thickness of the two water layers of the Sound, may be exposed to brackish-Baltic surface water as well as to the Kattegat water with its higher salinity. This means, further, that in summer the stock of animals living here is exposed to highly varying temperatures: higher temperatures when the area is washed by the surface water, and lower temperatures when the Kattegat water preponderates. The figures from the Lappegrunden off Helsingør (Brattström 1941, p. 92) show for June a temperature at 10 to 15 m ranging from 12.0° to 8.6° C., while the temperature at depths exceeding 20 m is below 7.1° C. For July the temperatures at 10 to 15 m range from 15.7° to 12.2° C., while the temperature at more than 20 m is below 8.9° C. These are only the average figures, but the temperature at these intermediate depths may often be considerably higher. The animal stock will often be exposed to warm Baltic water for a sufficiently long time to be induced to spawn.

These assumptions, based on our knowledge of the vertical distribution of the animals as compared with the hydrographical data, are supported by the occurrence of the larvae in the plankton. The stock living in more shallow water is induced to spawn earlier than the stock of the same species in somewhat deeper water, i. e. the spawning sets in gradually, not suddenly and violently, and is distributed over a longer period. Hence, their very long season in the plankton is characteristic of these larvae (cf. e. g. the larvae of *Nassa reticulata* (larvae occurring in the plankton during eight months of the year), *Acera bullata* (8 months), *Bittium reticulatum* (8 months), *Philine aperta* (8 months), and *Montacuta bidentata* (6 months)). The fact that such larvae are able to thrive in the plankton and to grow well within two-thirds of all months of the year in spite of the highly varying food conditions during this long period, seems to indicate an astonishingly adaptability in their development (cf. pp. 457—460). The spawning of most of these species begins simultaneously with the summer-spawning of the shallow water invertebrates, but the maximum of the former groups is generally reached somewhat later than that of the latter. Thus for most species the maximum occurrence of shallow water larvae is in June, while the species living at moderate depths have their maximum spawning in July—August. While the shallow water larvae decrease in number in late July and August, the larvae of the "intermediate species" are still frequent in September—October. In spite of the early spawning of these species, their most heavy spatfall is thus postponed to the late summer and autumn, i. e. to the same time as the earliest phase of the autumn spawning.

The autumn spawning (= "the Kattegat spawning"). The increase in temperature at a depth of 20 m takes place from June (average temperature at the Lappegrunden 7° C.) to August (11° C.), and the maximum temperature is reached in September (12.6° C.). At still greater depths the maximum temperatures are found still later in the year — at depths exceeding 30 m as late as November (BRATTSTRÖM 1941, p. 92). In accordance herewith the autumn spawning starts early in August with the first forerunners already in late July. The maximum of larval occurrence during this spawning is reached in September, and a characteristic feature of this spawning is the very large number of species taking part in it — much larger than in any other spawning in the Sound. The pump-series from $^{25}/_{8}$-1937 (cf. pp. 383, 388—89) comprised 44 species of larvae. Seven of these belong to shallow water forms, 10 to parents living at intermediate depths, and 27 to parents living in deep water, i. e. species belonging to the autumn-spawning.

The succession of dominant larvae is as follows (cf. fig. 197): The larvae of *Echinocardium cordatum* are already found in scattered specimens late in June, and are followed in July by the first few larvae of *Amphiura filiformis, Ophiura albida, Anomia squamula, Cultellus pellucidus,* and *Onoba striata*. The main spawning, however, in all these specimens does not set in until early in August. Besides the forms mentioned above, which form a characteristic element of the autumn-larvae, large numbers of accompanying larval species are present in the plankton from early August. Such species are e. g.: *Ophiocomina nigra, Magelona papillicornis, Poecilochaetus serpens, Odostomia turrita, Natica nitida, Alvania punctura, Lima loscombi,* and *Saxicava arctica*. Among the species which spawn in August are also some forms with a shortened pelagic larval life, viz. *Pomatoceros triqueter* and other forms with a totally non-pelagic larval development, e. g. *Exogone gemmifera* and *Sphaerosyllis tetralix*.

In contrast to the conditions prevailing during the summer-spawning, which comprised very large numbers of only a few larval species, the main part of the autumn-spawning is characterised by the large numbers of spawning species each represented in the plankton by a moderate number of larvae. Thus, in the first three months of the autumn-spawning there is no single dominant species of larva, but several species of nearly the same frequency.

In September nearly all the common larvae from August are still present in considerable numbers in the plankton supplemented by a few new larval species, e. g. *Brissopsis lyrifera, Ophiothrix fragilis, Autolytus prolifer* (swimming adults with larvae in the brood-pouch), *Eulimella nitidissima, Coecum glabrum,* and *Natica montagui*. None of them is very numerous. *Brissopsis* and *Coecum* are probably the commonest. The larvae of *Chaetopterus variopedatus* and *Phoronis mülleri* are characteristic "accompanying animals", and also larvae which are found in the plankton in all the months of the year seem to have a maximum occurrence in September to November, e. g. *Zirphaea crispata, Limapontia capitata,* and certain species of *Cyphonautes*. Among the bottom invertebrates with a non-pelagic development the Polychaetes *Stylarioides plumosa, Nicomache lumbricalis,* and *Trichobranchus roseus,* according to the size and state of ripeness of the eggs in the body-cavity, would seem to spawn in September; however, nothing definite can be stated.

September is the richest month of the year as regards the number of larval species in the plankton. A total of 103 species of larvae have been found in plankton from the Sound from this month (cf. pp. 398—400). The conditions in October remind us closely of those in September. The number of larval species is nearly the same (101 species known from the plankton in October), but the number of specimens is slowly decreasing.

This decrease in the number of larvae sets in very violently in late October, and in early November the number of larval species (56 species known from plankton) is reduced to about half that for September—October, and most of the larvae are only present in a few specimens. This is one of the minima of the year, but when the total sum of larvae is considered this minimum may be concealed by a sudden immense occurrence of larval Bryozoans (cf. e. g.

the graphs from Helsingor 1941, p. 377). Thus, taken as a whole, the first and largest part of the autumn spawning is brought to an end in late October and early November.

The last part of the autumn spawning, in late November, December, and January, shows quite different features from those found in August, September, and October. While the August—October spawning was characterised by a large number of species with a moderate number of larvae, the December—January spawning exhibits large numbers of larvae belonging to a few species, i. e. similar characteristics as are known from the summer spawning of shallow water forms (= "the Baltic spawning").

Apart from *Cyphonautes* the dominant larva during December—January is that of *Mya truncata*, which forms a distinct and pronounced maximum, because the main spawning sets in very suddenly. Two other species of larvae may be mentioned, which are of significance during these months, viz. those of *?Mysta barbata* and *Nephthys ciliata.* It seems curious that these three forms spawn so much later in the autumn than the majority of autumn-spawning species. If the spawning is induced by a rise of the temperature — and there are many indications that the temperature is at least a very essential factor for the spawning — it seems reasonable to explain the late spawning of *Mya truncata* by the burrowing habits of this species. *Mya truncata* is probably the deepest burrowing of all the invertebrates in the inner Danish waters, the animal itself often living 40 cm or more below the surface of the bottom with a long siphon reaching up over the mud. It is a matter of fact, however, that the temperature amplitude is much smaller in the mud than in the water mass above, i. e. the mud has a lower temperature than the water during the autumn months. Although water is constantly streaming into the pallial cavity of these Lamellibranchs, the lower temperature of the mud will probably reduce the water temperatures so much that the ripening of the eggs and consequently the spawning will be somewhat retarded. It seems impossible, however, to explain the late spawning of *?Mysta barbata* and *Nephthys ciliata* in the same way or to find any other relation to the temperature conditions, which make their late breeding season intelligible. Their special modes of feeding (cf. p. 412) make nevertheless these larvae well fit for a pelagic life at this unfavourable time of the year.

Already in late January this "indian summer" is on the decline. A new minimum sets in during February and March, but the last laggards are still present in March and April, when the first larvae of the spring spawning appear in the plankton, announcing the new year.

Species spawning throughout the year. A few species with pelagic larvae are met with in the plankton in all the months of the year. Such species are e. g. *Limapontia capitata* and *Zirphaea crispata.* But also in such larval stocks annual variations seem to occur: the maxima normally in late autumn (October—November), the minima in late winter (February and March) and, for *Limapontia,* also in the summer. Such larvae feed and grow during their planktonic life and seem to be able to develop and metamorphose at all times of the year in spite of the greatly varying conditions in the plankton at the different seasons. A quite similar occurrence all the year round with an autumnal maximum is known for certain larvae of the Nudibranchs and *Cyphonautes.* The Nudibranchs, however, have a very inconsiderable growth, if any at all, in the plankton and seem to be less dependent on the food conditions prevailing there, and accordingly their adaptability is less surprising than that of the planktotrophic larvae mentioned above. The larva of the Polychaete *Capitella capitata* is also found in all the months of the year, being "lecithotrophic" and thus independent of the contents of food in the water mass.

Besides the species mentioned above several forms with a non-pelagic development seem to breed all the year round. As our investigations have been especially focussed on the pelagic larvae, the spawning seasons in the Sound for species with a non-pelagic development are still rather little known. *Buccinum undatum* and *Neptunea antiqua* (developing on nurse eggs), and *Littorina saxatilis* and *Hydrobia jenkinsi* (both viviparous) seem to breed all the year round, and the same applies e. g. to the Polychaete *Fabricia dubia* (cf. p. 132), which develops the large yolky eggs in its tubes at all times of the year, and to the viviparous Nemertine *Prostoma obscurum* (p. 149).

A more intensive study will no doubt increase the number of known species behaving like these. Thus the egg capsules of *Lunatia pallida* (non-pelagic development, cf. p. 216) have been dredged in all the months from June to November and no doubt also occur later and earlier in the year, from which seasons only a few dredge hauls are at hand. It seems likely beforehand that such forms, in which the embryos are nourished on the surplus of food produced by their parents, will be quite independent of the seasons in the plankton.

9. Relations between Maxima of Pelagic Bottom Animal Larvae and of Phytoplankton in the Sound.

Elsewhere in this paper (cf. pp. 446—450) the food requirements of the different groups of planktonic larvae and the value of the different Phytoplankton organisms as food have been discused. With the facts here obtained as a starting point, the next thing will be to find the species in the plankton from the Sound which are of value as food for the bottom animal larvae. The tables of Steemann Nielsen (1937) showing the content of Phytoplankton at depths of 0 m, 5 m, and 15 m throughout the year off Snekkersten (calculated by the sedimentation-method with an Utermöhl-microscope) supplemented with net samples taken off Haken, Ven, all the year round (Cleve-Euler 1937) give a rather small number of species as dominants in the Phytoplankton of the Sound. Besides these species, which are directly mentioned, several other species are comprised by the terms "diatoms, peridinians, flagellates", etc. However, most of the dominant species are of no value at all as food for the bottom animal larvae. Thus, of the dominant Diatoms only *Skeletonema costatum, Rhizosolenia alata* var. *gracillima, Nitzschia delicatissima,* the small, not chain-building species of *Thalassiosira,* and perhaps the youngest stages of *Coscinodiscus radiatus* seem to be sufficiently small to serve as food for the larvae. The larger specimens of *Chaetoceras,* viz. *C. borealis, constrictus, contortus, curvisetus, decipiens, debilis,* and *laciniosus* measure 100 μ or more across the bristles, *Thalassiothrix nitzschioides* and *T. nordensköldi* as well as *Cerataulina bergonii* and *Eucampa zoodiacus* are large-sized, and the structure of their chains renders them unfit as food for the larvae. The Peridinians give the same result; *Peridinium corneum* (72—76 μ), *P. pellucidum* (45—68 μ), *P. pallidum* (70—90 μ), and *P. roseum* (50—58 μ) are too large. The same is the case with *Ceratium tripos* (200 μ) and *C. lineatum* (70—130 μ). — *Cyanophycea* are normally found in colonies and are consequently of no significance as food.

The last group mentioned in Steemann Nielsen's tables are the Flagellates (incl. unicellular green algae), but precisely these tiny organisms are extremely difficult to count in the samples. Several naked Flagellates cannot be preserved in any fixative known so far, and our knowledge of these organisms is further influenced by the fact that they are never taken in net hauls, and precisely these hauls have hitherto been used in the majority of plankton investigations (Steemann Nielsen 1938). The figures mentioned for Flagellates in the counts from the Sound should therefore be regarded as minimum figures only, but the occurrence and growth of several bottom animal larvae seem to show that the Flagellates and smaller Diatoms are present in sufficiently large numbers to constitute their food. Our task is now to see whether these small phytoplankton organisms are frequent all the year round or they have maxima and minima corresponding to those of the larvae.

However, before these questions are treated in detail a summary will be given of

The Conditions for Phytoplankton Production in the Sound.

The content of Phytoplankton in the Sound is directly dependent on the production of Phytoplankton: A. In the Baltic (Arkona-Basin), B. In the Kattegat, and C. In the Sound itself. The summary for these three areas given below is mainly based upon the papers of STEEMANN NIELSEN (1937 and 1940).

The production of Phytoplankton in the Baltic ("Arkona-Basin") is poor. From a minimum in January and February caused by the vertical movements of the water masses, the production sets in about the middle of March. The spring-maximum is reached early in April and consists mainly of Diatoms of small volume. *Skeletonema costatum* is a dominant. The number of Diatoms decreases during April and is immediately followed — in late April—May — by a maximum of small Flagellates. Such a maximum of small, mostly heterotrophic Flagellates occurs often after a Diatom-maximum. A fresh, but small, maximum with the small diatom *Thalassiosira nana* and Gymnodinians, Flagellates, and unicellular green-algae as dominants sets in during the actual summer time, but no maximum is found during the autumn months. The water masses near the southern entrance to the Sound contain still smaller quantities of Phytoplankton than the Arkona-Basin. The supplies of Phytoplankton carried to the Sound from the Baltic are, accordingly, poor.

The production of Phytoplankton in the Kattegat is fairly abundant. After a minimum in January a new production sets in at the surface in February, and a maximum is found in March—April to late July. Dominants in South-eastern Kattegat are (in February and March) *Skeletonema costatum, Thalassiosira nana, Nitzschia delicatissima,* and (in June—July) *Rhizosolenia alata* and *R. fragillima* together with several Flagellates and green algae. The two last-mentioned groups increase in number during July—August, when the Diatoms are decreasing. In September a new maximum occurs, consisting of Diatoms (dominants: *Chaetoceras sp., Leptocylindrus danicus* and *Skeletonema costatum*) together with large numbers of Flagellates and unicellular green algae. This maximum decreases during November, and nearly disappears in December.

The production of Phytoplankton in the Sound proper is extremely poor (STEEMANN NIELSEN 1937), viz. for the whole year only about $^2/_3$ of the production of one summer month in the northwestern part of the Kattegat. January and February show a pronounced minimum. A spring-maximum, with *Skeletonema costatum* and *Chaetoceras debilis* as dominants, is reached about the middle of March and disappears in late April. A new minimum from late April to medio May, during which only Flagellates are of any importance, is followed by a distinct but slight production from June to September with Flagellates and small Diatoms (*Skeletonema costatum* and *Rhizosolenia alata*) as dominants. From September this small maximum decreases until the minimum is reached in January—February.

The production of Phytoplankton within the Sound itself is, thus, too slight to support the stock of bottom animal larvae actually living in this area. "As to animals the northern part of the Sound is quantitatively a richer area than might be assumed from the quantity of organic matter produced by the phytoplankton within the area itself". The Kattegat water entering the Sound along the bottom (cf. this paper pp. 23—25) often contains large quantities of Phytoplankton as well as Zooplankton. "The stock of Zooplankton is accordingly only partially dependent on the production of Phytoplankton in the Sound" (STEEMANN NIELSEN 1940, p. 35, translated from the German). The same author is of opinion that rather large quantities of Phytoplankton may be carried to the Sound from the Baltic with northward-flowing currents during the spring-maximum (l. c., p. 39), and thus the production in this area — though poor — has also a certain significance for the bottom animal larvae in the Sound.

We are now sufficiently well informed of the production of Phytoplankton in the Sound and the neighbouring areas, and of the food value of the different species of Phytoplankton organisms to compare the stock of Phytoplankton actually found in the Sound during the year with the maxima and minima of the pelagic larvae. Owing to the different origin of the Phytoplankton, the two water layers will be regarded seperately. In the following survey the Phytoplankton organisms which are small enough to be devoured by the main stock of larvae, i. e. the Nannoplankton and the Ultraplankton, are marked with two asterisks, while the Microplankton organisms, known to be eaten by a few larger larval species only (*Polydora*, *Nephthys*, *Chaetopterus*) are marked with one asterisk. The data for the Phytoplankton are compiled from STEEMANN NIELSEN 1937 and CLEVE-EULER 1937.

January to the middle of March:

Phytoplankton: Pronounced minimum in both water layers. Inconsiderable amounts of **Flagellates. A few **Skeletonema costatum* and ***Rhizosolenia hebetata.*

Larvae: Pronounced minimum in February and early March. In January *Mya truncata* (Ultraplankton-feeder), *Nephthys ciliata* (now feeding on Lamellibranch-larvae), and ?*Mysta barbata* (lecithotrophic) are still frequent. Accompanying larvae are: *Glycera alba* (probably lecithotrophic, or — as the Indian species of *Glycera* — *Coscinodiscus*-feeder, cf. AIYAR 1933), and *Nerine foliosa.*

The middle of March to the middle of April:

Phytoplankton: A sudden spring-maximum sets in in the surface layers, shifting a week later to deeper water. Dominants are **Skeletonema costatum*, **Thalassiosira nordensköldi*, and **Chaetoceras debilis.* **Flagellates rather common. The production ceases a fortnight after having started, but Phytoplankton organisms are still present, though decreasing in number, in early April.

Larvae: A sudden maximum of *Polydora*-larvae. Especially *P. coeca* occurs regularly in immense numbers during the last half of March, and the larvae are large enough to feed on the larger diatoms present. Accompanying larvae: a few laggards of *Nephthys ciliata, Mya truncata, Nerine foliosa*, and *Glycera alba.*

The middle of April to June:

Phytoplankton: Surface plankton, also Flagellates, very poor until early May, when **Flagellates and small Diatoms (dominants ***Nitzschia delicatissima*) increase in number. In deeper water there are several Diatoms (dominants: **Leptocylindrus danicus, Chaetoceras sp.*, and a few ***Nitzschia*, ***Rhizosolenia hebetata*, and **Thalassiosira*) transported to the Sound with the Kattegat current. They increase in number towards the end of May.

Larvae: Surface plankton poor, with the first larvae of *Littorina littorea, Macoma baltica, Cardium edule,* and other summer-spawning species, increasing in number towards the end of May. In deeper water several larvae of a few species: *Ophiura robusta, Phyllodoce groenlandica, Myriochele danielsseni,* and *Aporrhais pes pelecani,* probably able to feed on the Diatoms drifted in from the Kattegat.

June—July—August:

Phytoplankton: In the surface layer there is a small summer maximum. As a whole this maximum is only slight, because nearly all the larger species are absent, but several small Phytoplankton organisms, of essential value as food for the larvae, occur in large numbers. Dominants are **Skeletonema costatum, **Rhizosolenia alata,* and, above all, **Flagellates and unicellular green algae. Diatoms are frequent in deeper water (dominants: various species of *Chaetoceras,* and, in July, ***Rhizosolenia alata*). Also **Flagellates are rather common here.

Larvae: The large summer maximum sets in at the surface early in June. Dominants: *Littorina littorea, Mytilus edulis, Mya arenaria,* with *Cardium edule, Macoma baltica,* and *Asterias rubens* as accompanying animals. The larvae increase in number during June, continue their maximum in July, and are still frequent, though decreasing in number, in August. — The larval stock in deeper water is rather poor in June. The first few forerunners of the autumn spawning appear in July, and early in August the main-spawning sets gradually in. Dominants are: *Echinocardium cordatum, Amphiura filiformis, Nassa reticulata, Cultellus pellucidus,* and *Onoba vitrea* with several accompanying animals: *Magelona papillicornis* (Lamellibranch-feeder), *Saxicava arctica, Lima loscombi,* etc. Most of these larvae increase in number during August.

September—October:

Phytoplankton: In the surface layers the **Flagellates predominate during September, while the Diatoms with **Skeletonema costatum* as the dominant species are less frequent. In October the surface is very poor in Phytoplankton. — At greater depths several Diatoms occur, with **Skeletonema costatum, **Nitzschia delicatissima, **Rhizosolenia alata,* and various species of *Chaetoceras* as dominants, and large numbers of **Flagellates (i. a. *Distephanus speculum*) originating from the autumn spawning in the Kattegat and carried to the Sound with the bottom current.

Larvae: Only a few larvae are found in the surface layers. Dominant is *Littorina littorea* (cf. the pump-series pp. 383, 388—89). — In deeper water the autumn spawning reaches its maximum in September, both as regards species and specimens. Dominant, besides the larvae mentioned from August, are *Brissopsis lyrifera, Ophiothrix fragilis, Coecum glabrum, Nassa reticulata, Philine aperta,* and several others. This maximum continues also in October, but decreases suddenly towards the end of this month.

November—December:

Phytoplankton: In November a varying but rather rich Phytoplankton is found throughout the water masses, especially small Diatoms, viz. **Skeletonema costatum* and ***Nitzschia delicatissima,* and **Flagellates. In December **Coscinodiscus radiatus* and other species of **Coscinodiscus* occur, while all other Diatoms decrease rapidly in number. **Flagellates are still rather frequent, especially at the surface.

Larvae: The last part of the autumn spawning sets in. Larvae of *Mya truncata* (Ultraplankton-feeder), *Nephthys ciliata* (feeding on large *Coscinodiscus*), ?*Mysta barbata* (lecithotrophic), and *Cyphonautes* are found throughout the water masses, with *Mya* as the absolute dominant.

Unfortunately the Phytoplankton tables of STEEMANN NIELSEN (1937) contain no exact figures for the Flagellates, because various groups of these seem to have been completely destroyed by the preservation (l. c., p. 16). Hence it has been impossible to prepare graphs for the occurrence of the Nanno- and Ultraplankton during the year, — a method which is much more instructive than that used here if we are to show the parallel with the larval maxima and minima.

The summary for the year given above shows, however, that the larval curves and the curves for the Nannoplankton and Ultraplankton are fairly parallel. The period January to the middle of March shows minima for the Phytoplankton as well as for the larvae; the maximum of large Diatoms from the middle of March to the middle of April sets in contemporaneously with a maximum of *Polydora*-larvae, the only larvae able to feed on these Diatoms. The period from the middle of April to June is rather poor in regard to the Phytoplankton as well as the larvae. The summer maximum of small Diatoms and Flagellates begins in June together with the summer-spawning of *Littorina littorea* and *Mytilus edulis*, and both maxima decrease towards the end of August. The maximum of Diatoms and Flagellates in deeper water drifted in from the Kattegat in September and October occurs simultaneously with the large numbers of larvae from the autumn-spawning. And finally — in November to December — there is a decrease in the larvae as well as in the Phytoplankton and an increase of large *Coscinodiscus* and of the only larva able to feed on them, viz. *Nephthys ciliata*.

AIYAR (1933) in his interesting paper on the Polychaete-larvae in the Madras plankton states that the larvae here crowd in November to March, "and this is the period, when the phytoplankton is also abundant". However, it is impossible to judge from his paper whether he has a sufficiently certain basis for his statement.

It has previously been suggested (pp. 400—408) that the summer-spawning and the autumn-spawning of the bottom invertebrates in the Sound are induced by a large rise in the temperature, so it could not be taken for granted that the larval maxima would fluctuate in parallel with the quantities of food present. The summary given above seems, however, to show that this is roughly the fact. In other maxima, e. g. those of *Polydora*, the coincidence with the temperature seems to be much less pronounced — or even dubious. In a few cases it cannot be totally excluded that spawning may be induced by other factors also, e. g. by a maximum of Phytoplankton. Thus MIYAZAKI (1938) has found that an extract of green algae (*Ulva*, *Enteromorpha*) may induce spawning in ripe Lamellibranchs (cf. the discussion on pp. 423—425). These things are, however, still so poorly known that a detailed discussion seems only of little interest at the present day.

It must be remembered, however, that while the large crowds of larvae occurring at the same time, i. e. as competitors in the plankton, are dependent on (e. g. restricted to a period with) a large quantity of food, i. e. a maximum of Nannoplankton and Ultraplankton, the individual larva of a crowding species is able to find sufficient food also outside the main season. The occurrence of such larvae as *Nassa reticulata*, *Bittium reticulatum*, *Aporrhais pes pelecani*, and *Philine aperta* during 8 or 9 months of the year, and the occurrence of larvae of for instance *Limapontia capitata* and *Zirphaea crispata* throughout the year (all of them Nanno- and Ultraplankton feeders), i. e. during seasons with pronounced maxima as well as minima of Phytoplankton, testify to a very large adaptability to the varying conditions of food.

10. The Recruiting of the Animal Stock of the Sound.

After the pelagic larval development and its problems have now been considered in general, it seems natural to finish the survey of the Sound with a discussion of the fauna of invertebrates occurring in the Sound proper, where most of our observations and experiments were made. The percentages of species with a pelagic or a non-pelagic development, the recruiting of species from parents occurring within the area or in neighbouring areas are questions which we are now able to reply in broad features.

The representatives of the four large groups in the Sound which have been the main subject of the present investigation, show the following data as to their mode of larval development (long pelagic, shortened pelagic, or non-pelagic development):

Systematic group	Number of species known from the Sound	Species of unknown larval type	Species with a long pelagic larval life	Species with a short pelagic life or a non-pelagic development
Echinoderms	32	6	23	3
Polychaetes	143	69	41	32
Prosobranchs	69	8	35	26
Lamellibranchs	61	12	38	11
Total...	305	95	137	72

It appears from the table that about one-third of the species of invertebrates examined reproduce in a non-pelagic way or with a very short free-swimming stage. This stock of animals is, accordingly, recruited from parents occurring within the area itself. Even when the smaller groups of invertebrates in the Sound are included in the calculations, the figures seem to range about the same orders of magnitude. Some of the groups have a majority of species with a non-pelagic or a shortened pelagic development (e. g. the Nemertines, the Nudibranchs, and the Bryozoans), others show a dominance of species with a long pelagic larval life (e. g. the Decapods, Cirripeds and the *Membranipora*-group within the Bryozoans), etc.

The remaining two-thirds of the species of invertebrates in the Sound seem, thus, to pass through a long pelagic life. It has been calculated that in summer and early autumn these pelagic larvae spend about 3 weeks, and in winter up to two or even three months, in the plankton (cf. p. 455). Such larvae have, accordingly, good chances of being transported with the water masses to other seas, and the Sound has good chances of receiving such "foreign" larvae, which may constitute an essential element for the recruiting of the invertebrate stock on the bottom. Conditions for such a supply of larvae from outside areas are especially favourable in the Sound, where two different water masses, both with a considerable renewal of the water, give rise to strong currents to and fro.

The stock of invertebrates in the Sound is accordingly composed of three different categories of young, viz. those originating from parents occurring in the Sound itself, those originating from parents in the Baltic, and those originating from parents in the Kattegat.

The young originating from the Sound itself comprise mainly those which develop in a non-pelagic way. Several larvae, however, have a free-swimming life of a few hours to a few days only, that is to say larvae of this type produced in the Sound will generally metamorphose and settle before they are carried away from the area in question. Examples of such larvae are: Serpulid larvae, *Terebellides strømi, Hydrobia ulvae, Turritella communis,* and several Nudibranchs. The larvae of *Rissoa membranacea* must also be referred to this category. Under normal conditions they spend their pelagic life in the *Zostera*-meadows, where the movements of the water are rather slight (SMIDT 1938). The *Balanus* larvae seem also to a certain degree to swim about and develop near the substratum of the adults.

The young originating from the Baltic are closely associated with the surface water, viz. the Baltic current. During a period with a constant north-flowing current this surface layer in the Sound may be renewed in less than three days (STEEMANN NIELSEN 1940, p. 33). The northward-flowing current is strongest in May (24 c.km northward-flowing water per month, JACOBSEN 1925), and precisely at this time the spawning season begins in the Baltic and in the surface layers of the Sound, to continue in June and July. Owing to these strong northward water movements during the breeding seasons of the Baltic animals it is probable that a great many of the surface larvae in the Sound originate from parents living in the Baltic. To this number may be added several larvae in the youngest stages produced within the Sound itself, viz. Lamellibranch larvae, the veligers of which occur in the plankton already 12—48 hours or earlier after the eggs have been fertilised, Prosobranch larvae, and several Polychaete larvae which, having developed within egg capsules or egg masses, suddenly hatch and appear in the plankton as fully developed veligers (cf. p. 395). However, most of these small larvae will be carried to the Kattegat by the surface current before they have reached the stage of metamorphosis, and it seems most likely that a rather great part, probably even the main part, of the populations of *Littorina littorea, Mytilus edulis, Macoma baltica, Cardium edule,* and *Mya arenaria* in the Sound is recruited from Baltic larvae. The Baltic bottom fauna, however, is only a depauperated outpost of the shallow water fauna in the Sound and accordingly the Baltic current has no possibilities of carrying new species to the Sound (cf., however, *Neritina fluviatilis* p.166). The main function of the Baltic current for the larval ecology of the Sound seems to be: to remove all or most of the young pelagic larvae produced in the surface layer in the Sound itself and to replace them by a depauperated number of older larvae produced in the Baltic.

The young originating from the Kattegat constitute undoubtedly the most essential stock in the Sound north of the threshold Amager—Limhamn. The pump-series have shown that by far the majority of all the pelagic larvae in the Sound are associated with the Kattegat layer. The percentage of larvae associated with this layer is even larger off Helsingør than off Ven, probably constituting more than 90 per cent of the total stock of planktonic larvae of the whole year (cf. p. 390). In a previous chapter of this paper it has been shown that 50 per cent (or probably much more) of the whole stock of pelagic larvae in the Sound originate from parents in the Kattegat (pp. 378—379), and that the Kattegat larvae constitute the absolutely dominating element in the plankton both as regards species and specimens.

From an ecological point of view it is reasonable to designate the Sound as a typical outpost of the Kattegat, camouflaged by a thin brackish layer at the surface.

But from what part of the Kattegat do these larvae originate? Are they derived from parents living in the southern or the northern part of Kattegat or even from parents in the Skagerrak or more remote seas?—We have two groups of information which allow us to go into this question, viz. the speed of the southward-moving stream and the length of the pelagic larval life.

When the northward-moving surface stream in the Sound is strong, it will immediately give rise to a strong southward-moving stream along the bottom (Aage Jensen 1940, p. 8). It has been stated above that the northward-moving surface stream is strongest in the summer (May) and weakest in the winter (November) (Jacobsen 1925), and this is in good agreement with Aage Jensen's calculations, viz. that during the period from July to September a certain water mass will take 1 to $1^1/_2$ months, and during the period from January to March about $2^1/_2$ months, to move from the Skagerrak to the entrances of the Belts and the Sound.

The average duration of the pelagic larval development in our seas is about 3 weeks in summer and 2 to 3 months in winter. This, in connection with the fact that most larvae met with in the Sound plankton are in a late stage of development but still without any indications of metamorphosis, i. e. larvae which in summer have spent on an average two weeks and in winter on an average $1^1/_2$ months in the plankton, seems to show that most of the larvae carried to the Sound from the north originate from the southern and middle parts of the Kattegat. To these may, however, be added such larvae as are at least occasionally able to metamorphose in mid-water and to continue their pelagic life afterwards (cf. pp. 466—467). An estimate gives the result that such a mid-water metamorphosis may prolong the pelagic life with about one month on an average. On pp. 370—371 it has been calculated that a single larva of a species found in a main-series in the Sound may correspond to one and a half milliard of specimens in the Sound on a particular date. The same calculation is of course valid for young, metamorphosed in mid-water. Such "pelagic bottom stages", although only found in a few specimens in our collective main-series, may, therefore, be of no little significance in the Sound. And such larvae, when found in summer and autumn plankton, may probably originate from parents in the northern Kattegat or Skagerrak, and it cannot be totally excluded that even larvae from the North Sea may on certain favourable occasions contribute to the invertebrate stock in the Sound.

Most of these transports from the Skagerrak to the Sound and the Belts comprise rather large water masses, which will probably contain numerous larval elements of each species. Hence it can be taken for granted that large numbers of foreign larvae are regularly transported to the Sound, among others such larvae the adults of which do not live in the Sound. A selection takes place between all the larvae introduced, and the slightest changes in the hydrographical conditions or bottom conditions in the Sound may cause the settling of new species of larvae or the perishing of young stages of species which have earlier been able to settle in the Sound.

Our main-series include several species of larvae, most of them in late stages, the parents of which have never been met with in the Sound. Examples are: *Echinus esculentus*, *E. acutus*, *Spatangus purpureus*, Spionid larva A, B, C, D, E and F, the larva of *Mystides sp.*, *Poecilochaetus serpens*, *Alvania punctura*, *Coecum glabrum*, *Aclis minor*, *Odostomia conoidea*, *Mangelia attenuata*, and *Philbertia linearis*. Most of these larvae occurred regularly year after year in our main-series, often in fairly large numbers. Nevertheless they do not settle, or at any rate they do not grow to the adult stage, in the Sound proper. (Only *Coecum* has probably been overlooked in the adult stage). Under extraordinary conditions, however, they will get a chance to settle. Example: In a bottle-collector off Ven, depth 16 m, a young bottom stage of *Porcellana longicornis* was found. The larva as well as the bottom stage had hitherto been unknown from the Sound.

Besides these species of larvae which do not settle in the Sound, another stock of northern larvae occurs which may now and then find a chance to settle, but which seems to be so rare in the adult stage that the adults must be regarded as casual survivers from the larval swarms transported to the Sound. Examples are: *Ophiocomina nigra, ?Mysta barbata, Nerine foliosa, Magelona papillicornis, Lanice conchilega, Eulimella nitidissima, Natica montagui,* and probably also *Phoronis mülleri.*

The fact that the combination: high salinity — sandy bottom — vegetation, as well as the combination: low salinity — clayey or muddy bottom — no vegetation are rare in the Sound, is probably one of the main causes of the death of several larvae.

However, the stock of larvae carried to the Sound is so rich in species and so luxuriant that the conditions for a renewal of the actual fauna as well as for a change to another composition of the fauna are constantly present. It has been mentioned above that e. g. artificial substrata placed at the right depth and in water of a suitable salinity may induce larvae to settle which will not normally metamorphose in the Sound.

And now we know by far the majority of the planktonic larvae occurring in the water masses of the Sound. Their identity and their season of occurrence as well as their relative frequency have been studied and noted down for a series of years.

Thus we have reached the phase in our marine investigations in which experiments with the individual species of larvae may be commenced. Studies on the metabolism of the planktonic larvae in order that we might learn the size of their food requirements will throw light on one of these phases (these studies, which have been undertaken at the Helsingør laboratory by Mr. ERIK ZEUTHEN, will be published by him in a special paper). — Another point of essential interest is the study of the young, just metamorphosed bottom stages and their mutual competition. Experimental tanks and dishes with different substrata placed in suitable and well selected localities and depths within the Sound will show the conditions under which the different young have their optimal and minimal growth. By varying the periods during which such experimental tanks are exposed in the water, it will be possible to vary the composition of the stock of young which settle in the dishes. Thus, in winter and spring seasons the populations may develop without Echinoderms as competitors; experimental tanks in Baltic water may be exposed at seasons during which *Littorina littorea* and *Mytilus edulis* dominate or at seasons during which they are totally absent, etc.

Such an analysis, though difficult and troublesome, seems now to be practicable, and precisely such an analysis is an absolute presupposition if we are to understand the composition and ecology of the animal communities, and to be able to judge whether they are identical with biocoenoses, and to acquire a knowledge of the first simple lines of the competition on the sea bottom.

VI. Some Outlines of the Ecology of Reproduction and Larval Development of Marine Bottom Invertebrates.

1. Problems of Spawning and Fertilisation.

The mode of reproduction of the adult invertebrates is of fundamental significance for the fate of the larval stock produced. The size of the "waste" in a larval stock may depend on several factors closely associated e. g. with the mode of fertilisation in the parents, the way in which the embryos are protected, and the space of time spent before the embryos hatch and have to feed on the plankton. It seems reasonable, therefore, to briefly discuss here some of these factors.

The mode of fertilisation.

Copulation is the most certain method of fertilisation of the eggs. As regards the invertebrates of the Sound this method is known for *Capitella capitata*, all the higher Prosobranchs (i. e. *Lacuna*, *Littorina*, *Rissoa*, *Hydrobia*, *Nassa*, *Buccinum*, *Neptunea* etc.), all the Opisthobranchs, for the Cephalopods and all (or nearly all) the Crustaceans. Copulation, however, is unknown in all the northern Echinoderms, nearly all the Polychaetes, several primitive Prosobranchs, and all the Lamellibranchs. -When copulation takes place, sperm as well as eggs are totally independent of the environment of the copulating animals. The sperm is introduced directly or in spermatophores into the genital duct of the female, i. e. the spermatozoa are transferred to conditions under which they will have a good chance of finding an egg of their own species; their activity will be stimulated, and hence a 100 per cent fertilisation of the eggs seems to be possible. A further consequence of the fertilisation within the mother animal is that the eggs may be better protected against the surroundings also after the fertilisation and during the development of the embryos. They may for instance develop inside the mother by viviparity or by different forms of internal brood-protection, or they may already in the oviduct be surrounded by a more or less thick and resistant capsule or gelatinous mass, which protects them against infections by infusorians and bacteria, or attacks by larger carnivorous enemies. Eggs which are to be fertilised freely in the water, must be spawned in a state which allows the spermatozoa to "attack" them, i. e. they are much less protected against infusoria and bacteria than eggs fertilised within the mother animal.

Some of the invertebrates which have no actual copulation have, however, a "pseudo-copulation", which seems to include nearly all the advantages known for the real copulation. In the genera *Amphiporus* and *Lineus* (Nemerteans, both known from the Sound) the male and female secrete a common mass of slime, and spawn, imbedded in this, their eggs and sperm. Thus the fertilisation takes place under just as favourable conditions as those found within the oviduct itself, no sperm is lost, and the eggs are laid imbedded in slime. In other genera of Nemerteans, e. g. *Carcinomemertes*, the spermatozoa from such "pseudo-copulating" species will push through the slime and into the oviduct or even the ovary of the female (Coe 1902, 1943 p. 265). In the Nemertean *Micrura alaskensis* up to 50 specimens may spawn together in a narrow coil surrounded by slime (Coe 1901). In the Polychaete *Scolecolepis fuliginosa* several specimens will form a common mass of slime, in which they spawn their sperm and eggs (Claparède & Metschnikoff 1869). Another form of "pseudo-copulation" is found in the Terebellid *Nicolea zostericola* (Northern seas, not in the Sound), in which the male swims to the mouth of the female tube, spawning its sperm between the tentacles of the female, which at the same time spawns its eggs in a slime, which hardens to a cocoon twenty minutes later (Herpin 1925). It must be assumed, though it has not hitherto been stated, that several other Polychaetes have a similar "pseudo-copulation", especially such species as deposit their eggs in regular capsules (e. g. *Polydora)*, and probably also several of the species which deposit their eggs in gelatinous masses.

However, also some of the species which shed their eggs freely in the water seem to economise with their spermatozoa as much as possible. In the non-Danish Polychaete *Aricia foetida* the male fertilises the eggs at the moment at which they are spawned (cf. this paper p. 77). In the Actinian *Sagartia troglodytes* a male and a female specimen, when going to spawn, will move towards each other and will not shed their sexual products until they are quite close to each other (Nyholm 1943, p. 172—74). In the Prosobranchs *Helcion pellucidum* (Ankel 1936 a) and *Gibbula tumida* (Gersch 1936) the male and the female are sitting close together during the emission of sperm and eggs. This is probably the case in several other species also. In such species the sperm is shed in the direct vicinity of the eggs, but the sperm is exposed to the water masses before reaching the eggs and may be weakened or even destroyed, e. g. if influenced by brackish water (cf. p. 445). Von Medem (1942) found for *Patella coerulea* and *P. lusitanica* at Naples (which probably, like the northern *Patella vulgata,* spawn eggs and sperm freely in the water) that the presence of a male or a female body of its own species is required if the sperm spawned is to attain its full activity, while sperm suspended in sea water far from any adult specimens will cease to move. This observation supports the conjecture that crowding in such species is of essential value for the process of fertilisation. — In the Echinoderms, also, such tendencies seem to exist. Tennent (1910) mentions crowding habits in spawning specimens of *Toxopneustes variegatus,* and Orton (1914 a) observed at Plymouth that ripe specimens of *Psammechinus miliaris* were often found sitting two and two closely together — occasionally three or more. More than two-thirds of all "pairs" examined consisted of a male and a female specimen. Mortensen (1943, p. 136), however, questions the conclusions of Orton, regards the crowding beneath stones as a shelter against the light, and recommends observations on crowding specimens also outside the breeding-season.

A very large number of species — probably by far the majority — spawn their eggs and sperm freely in the water where the fertilisation takes place. This is the case with most *Actinia,* several *Polychaeta,* nearly all the *Echinodermata, Placophora* and *Lamellibranchiata,* and the most primitive genera of the *Prosobranchiata.* With the results stated above in mind, this method of fertilisation seems extremely extravagant. The sperm is directly exposed to the water masses and may here be the subject of a catastrophe, e. g. when the salinity is too low to activate the sperm (cf. Mortensen 1920, 1938, and this paper p. 445). Also when the salinity and temperature are optimal, the sperm will spread in the water masses, and large quantities of sperm might be assumed to perish without having met with an egg of its own species. But also the eggs seem to have rather poor chances when shed freely in the water. Dispersed by the movements of the water, it seems likely that their chance to meet with spermatozoa of their own species in the huge water masses within the relatively short space of time during which the individual egg is able to be fertilised is rather poor. However, this is not the case! The list given elsewhere in this paper (pp. 443—446) shows clearly that it must be regarded as a rule that the ripe females of most marine invertebrates will not spawn until they are induced to do so by swarms of sperm of their own species which form a "sexual milieu" round them. When such conditions are absent, the females, though ripe, will often retain their sexual products for months or for a whole year. Females which are induced to spawn by swarms of active sperm have therefore, also when the eggs are shed freely in the water, a very good chance of having them fertilised, and the "waste" of eggs seems to be considerably reduced owing to this spawning mechanism. — The dispersion of the sperm, the danger that the sperm may be immobilised by the influence of brackish water, and the fact that the freely laid eggs are exposed to attacks from Infusorians and Bacteria seem to be the main disadvantages of this spawning method.

The mode of spawning:

Viviparity, — the highest degree of brood-protection — seems to be of little importance in the invertebrates in our seas. In the Sound it is known for the Actinian *Hormathia digitata*, the Echinoderm *Amphipholis squamata*, the Polychaete *Dodecaceria concharum forma A*, the Nemertean *Prostoma obscura*, and the Prosobranchs *Littorina saxatilis* and *Hydrobia jenkinsi*. In the three last-mentioned species and in *Amphipholis* viviparity has been observed in specimens from the Sound, while viviparity for the two remaining species has been recorded from other localities in the available literature. *Prostoma obscura* and *Hydrobia jenkinsi* are brackish-water animals, and can hardly be regarded as true marine species. Further, it cannot be excluded that under special brackish water conditions *Nereis diversicolor* may reproduce by viviparity. Also *Nereis dumerili*, which normally reproduces by larvae, is occasionally found to be viviparous in certain localities (HERPIN 1925). Viviparity in the two latter species, however, has not hitherto been recorded from Danish seas.

Brood-protection is found in several different modifications and in several different groups in the Sound. Examples from Danish seas are: *Henricia sanguinolenta, Asterias mülleri, Exogone gemmifera, Exogone verugera, Sphaerosyllis tetralix, Autolytus prolifer, Miroserpula inflata, Crepidula fornicata, Ostrea edulis, Montacuta bidentata* and *M. ferruginosa, Pholas candida, Teredo navalis,* and all the *Isopoda, Amphipoda,* and *Decapoda.* Other examples in which the brood-protection is of a somewhat more primitive type are: *Harmothoë imbricata* and *H. impar* (eggs in a thin gelatinous layer beneath the elytra), *Notophyllum foliosum* (egg string on the back partly covered by the dorsal cirri), *Capitella capitata, Polydora ciliata, P. coeca, Pygospio elegans, Nereis dumerili, Fabricia dubia, Filograna implexa, Spirorbis borealis, S. spirillum, S. granulatus* (all with eggs and embryos laid in the tubes of the parent, which perform the renewal of the water), *Modiolaria discors* (egg string around the mother animal in a "nidus"), and the species of Cirripeds, e. g. *Balanus* (eggs developing in the body cavity until the Nauplius-stage is reached). From the Polychaetes, which protect their eggs in their tubes, all transitional stages are found, through the faintest traces of brood-protection to such Polychaetes as fasten their gelatinous egg masses to the mouth of their tubes without protecting them at all. Three species of Lamellibranchs, all of common occurrence in the Sound, according to the literature have occasionally been found with fertilised developing eggs in the mantle cavity, viz. *Mya arenaria* (VLÉS 1909), *Mya truncata* (OSLER 1826), and

Zirphaea crispata (Bouchard-Chantereaux 1879). The same is known for *Cuspidaria cuspidata* (Grobben 1892), a species which is rather common in the Kattegat. All four species in question are among the highly organised Lamellibranchs with coalescent mantle lobes and long or rather long siphons. A few eggs have probably accidentally been retained in the mantle cavity after the spawning and have been fertilised by spermatozoa introduced with the water current to the gills. This brood-protection must accordingly be considered a false one.

Eggs laid freely in capsules attached to a substratum. This spawning method is known for several species within the Sound, especially the Polychaetes viz. *Spio filicornis* and several other *Spionidae*, several Prosobranchs, e. g. all the *Rissoidae*, *Littorina littorea* (pelagic capsules), *Turritella communis*, *Coecum glabrum*, *Scala clathrus*, *Pelseneeria stylifera*, and all species examined within the genera *Trophon*, *Nucella*, *Sipho*, *Neptunea*, *Buccinum*, *Nassa*, *Bela*, *Philbertia* and *Mangelia*, and in the Cephalopod genera *Rossia* and *Sepietta*. The hatching embryos, whether pelagic or non-pelagic, will often leave the capsule through a preformed exit hole or through a special, softened part of the capsule, which is easy to pierce.

Eggs laid freely in gelatinous masses or strings, attached to a substratum. Spawns of this type are laid by a very large number of invertebrates in the Sound, viz. the Polychaetes *Phyllodoce groenlandica*, *Eulalia viridis*, *Scoloplos armiger*, *Cirratulus cirratus*, *Owenia fusiformis*, *Terebellides strømi*, *Dasychone bombyx*, several Nemerteans, the Prosobranchs *Acmaea testudinalis*, *Gibbula tumida*, *Lacuna divaricata*, *Lacuna pallidula*, *Littorina obtusata*, *Hydrobia ulvae* and *H. ventrosa*, *Turritella communis*, *Bittium reticulatum*, *Triphora perversa*, *Capulus hungaricus*, *Brachystomia rissoides*, the Tectibranchs *Actaeon tornatilis*, *Retusa truncatula*, *Acera bullata*, *Philine aperta*, *P. scabra*, *Aplysia punctata*, *Limapontia capitata*, all the Nudibranchs, the Lamellibranch *Modiolaria nigra*, and the Cephalopod genera *Loligo* and *Alloteuthis*. Also the sand-incrusted, flat egg rings of hardened slime known for all species of the genus *Natica* may be referred to this type of spawn. — In some species the embryos will feed on the slime in which they are imbedded, in other cases the slime is only of value as a protecting layer.

Eggs shed singly and adhering separately to a substratum. Spawns of this type are known for the Placophores *Chiton cinereus* and *C. marginatus* (often several eggs attached close to each other), for the Prosobranchs *Aporrhais pes pelecani* (Lebour 1933 a), and for the Lamellibranch *Cardium exiguum* (Lovén 1870). In these species the eggs are surrounded by thick, gelatinous, sticky envelopes, which fasten them to a substratum. As eggs of this type are very difficult to find and to identify under natural conditions, the species mentioned are the only representatives hitherto known for this type of spawn. It has, however, been stated that *Macoma calcaria*, *Astarte borealis*, *A. montagui*, and *A. elliptica* (all living in the Sound) have gelatinous envelopes of quite the same type as found in *Cardium exiguum* (Thorson 1936), and it is probable that they adhere to their substratum in a similar way as this latter species. A closer investigation will probably add a large number of species to this poorly known group.

Eggs shed singly and developing suspended in the water masses or floating along the bottom. Known for most Echinoderms, several Polychaetes, e. g. in *Nereis pelagica*, *Nerine foliosa*, *Chaetopterus variopedatus*, *Pectinaria koreni*, *Ampharete grubei*, *Nicolea venustula*, *Arenicola marina*, and *Thelepus cincinnatus*, most *Placophora*, the most primitive Prosobranchs, e. g. *Acmaea virginea*, *Helcion pellucidum*, and *Gibbula cineraria*, and the majority of the Lamellibranchs. This spawning type is of great significance in our seas. The mode in which the eggs are shed varies considerably. In some species the females spawn resting on the bottom or on their substratum (Echinoderms, several Polychaetes, Nemertines, Placophores, Lamellibranchs, Prosobranchs and Cephalopods). In other species the parent animals spawn swimming at the surface (epitoquous forms of the *Syllidae, Nereidae, Eumeniidae, Cirratulidae,* and a few species of the *Hermionidae, Phyllodocidae, Amphinomidae.* and *Scalibregmidae*) (not observed in the Sound, but cited from literature dealing with specimens from seas outside Denmark). — The newly spawned eggs may be "true pelagic", with vacuoles which make them able to float in the water (known for a few genera of Polychaetes only, viz. *Nerine, Scolecolepis* (small gelatinous nest at the surface), and *Poecilochaetus*), or they may be somewhat heavier than the water but stirred up and suspended by the slightest movement of the water masses. To this type belong by far the majority of the "pelagic eggs"; in aquaria they will therefore sink to the bottom, but in the sea they will normally be suspended in the water like "true pelagic" eggs. — Nearly all such eggs found in the water will develop into pelagic larvae. Exceptions are e. g. the eggs of *Arenicola marina, Ampharete grubei* and *Thelepus cincinnatus.*

2. Spawning Inducements and the Surrounding Conditions.

It has been shown (pp. 443—446) that spawning in the females of marine bottom invertebrates is often induced by sperm from their males. The males, however, may also be induced to spawn when surrounded by eggs or "egg-water" from a female of its own species (GALTSOFF 1940), but the spawning inducements starting the spawning in the first males of a stock are, no doubt, one or more factors in the environment.

A. The food conditions,
which are, of course, of fundamental value for the growth of the species and accordingly also for the surplus of organic matter allowing the adult specimens to produce their sexual products, seem to be of little or no value as a direct inducer of spawning and breeding. ORTON (1920, p. 341), having examined the Ascidians *Leptoclinium gelatinosum* and *Bothryllus violaceus* at Plymoth, states that "the beginning and the ending of the breeding period" (namely the summer season) are "coincided with approximately the same sea-temperature, and since a large growth occurs in this species during the winter, the factor of food in determining breeding can be eliminated". This and several other experiences in regard to marine invertebrates seem, according to ORTON (l. c.), to be sufficiently striking to warrant a generalisation of the results. Changes in the salinity seem also, according to ORTON, to be of no or little value as a spawning stimulus.

B. The temperature
of the sea-water is normally regarded as the most essential factor in starting the breeding seasons. Several authors have discussed these problems, first of all APPELLÖF (1912) and ORTON (1920). The latter author states on the basis of the notes on breeding seasons in invertebrates from Naples, Plymouth, and River Clyde "that most animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, namely at either the maximum or the minimum temperature of the locality". This rule in connection with the examples given by ORTON (l. c.) are in good agreement with nearly all the breeding conditions known for the Sound. The two largest spawnings in the Sound, viz. the summer spawning and the autumn spawning, both set in after a considerable rise of the temperature and reach their maximum when the water temperatures round the adults are at their height (cf. pp. 402—406). A few deep-water species have their main spawning

at very low temperatures, e. g. in April, when the temperature rise is only $^1/_2$° C. over the minimum for the year (cf. p. 401), thus corresponding to ORTON's breeding seasons "at a definite temperature change". Our observations on the larvae of *Polydora ciliata*, which may occur in the Sound in March as well as late in the summer, i. e. during periods with pronounced minimum and maximum temperatures, correspond to ORTON's data for *Patella vulgata*, which at Plymouth spawns at maximum as well as at minimum temperatures. Also such species as spawn throughout the year in the Sound (cf. p. 407) at any temperature occurring there may be comprised by ORTON's rule. They have only a larger lability than the other groups of breeders, i. e. their temperature amplitude for breeding is never surpassed in the waters in which they live.

However, far from questioning the exceedingly interesting main results of ORTON, which have further been supported by the observations from the Sound, I think it worth while to discuss a few of the points in detail. Thus it seems necessary to me to distinguish between temperatures which allow the animals to ripen their sexual products, and temperatures which actually induce the animals to spawn. ORTON (1920, p. 340) says, regarding these two phases as a whole, that "the extrusion of ripe ova, or the fertilizability of eggs with subsequent development, is taken as the criterion of breeding". I cannot agree with him in this. Many marine invertebrates may contain ripe or nearly ripe sexual products also outside the breeding period. Thus ripe active sperm may be found in several species throughout the year in spite of a limited breeding season, and also female specimens may contain eggs ready to be spawned for months or even longer without shedding them. In several of such species the eggs will not ripen until they have been suspended in the water for a few minutes to a few hours. Examples: *Pecten opercularis* was sexually mature in late February, but spawning took place in July—August (Firth of Forth, FULLARTON 1890). In *Tellina crassa* the breeding period is in summer, but ripe sperm and eggs were also found in January. Specimens of *Cardium crassum* contained "apparently ripe eggs and sperm found in almost any month. Larvae are taken in the plankton through spring and summer, and are often plentiful" (LEBOUR 1938, p. 124). In East Greenland the species of *Astarte* (*borealis, elliptica, montagui*) contain ripe eggs and active sperm during the summer, but spawn in late autumn or in winter (THORSON 1936). It can hardly be doubted that such eggs may be artificially fertilised with subsequent development also outside the actual breeding season. Also the large literature on the embryonic development in marine invertebrates seems to show, that successful artificial fertilisation may take place earlier in the year than the actual breeding season. The temperature required for an inducement of the spawning seems thus to be another than that required for a ripening of the sexual products, and it cannot be totally excluded that near the limit of its area of distribution a species, at least when recruited by pelagic larvae, will have a small area where it is able to ripen its sexual products, but not to spawn them. — GALTSOFF (1940) states, after several thorough experiments on the physiology of reproduction in *Ostrea virginia*, "that there exists several "critical" temperatures for spawning of males and females, apparently determined by their physiological conditions", and gives here a weighty view for further discussions.

The significance of the temperature as a limiting factor for the ripening and spawning and accordingly the distribution of most marine invertebrates is thus unquestionable, but it cannot be taken for granted that the actual area of distribution of a species coincides with the area in which the temperature is suitable for spawning. APPELLÖF (1912) has pointed out that the vegetative processes are less dependent on the temperature than the reproduction and development, and our present knowledge seems fully to corroborate this. Marine invertebrates in the pelagic stage carried by the currents to other sea-areas may often vegetate there without being able to ripen and spawn their sexual products. But also in places in which the sexual products ripen and are spawned, the larval development may be impeded. PELSENEER (1901, p. 288) has shown that the adults of marine invertebrates are more resistant to extreme temperatures than the larvae, and the same author and later on SVEN RUNNSTRÖM (1927 a, p. 40) have shown that the first cleaving stages are much more sensitive to extreme temperatures than the older, free-swimming larvae. These observations comprise several invertebrates which are common also in the Sound, such as: *Strongylocentrotus droebachiensis, Echinus esculentus, Psammechinus miliaris, Echinocyamus pusillus, Echinocardium cordatum, Asterias rubens, Littorina littorea, Littorina obtusata, Nassa reticulata, Lacuna pallidula, Mytilus edulis, Dendronotus arborescens, Scoloplos armiger, Balanus balanoides,* and *Crangon vulgaris.* — Thus, as regards temperatures, the youngest stages of development seem to be the most sensitive stages within the whole life-cycle of the species, and only under conditions which allow also these stages to develop normally will a population be able to maintain itself by its own brood.

The temperature seems, thus, to be the cause of the following limits of distribution of a species: A wide area, in which the animals may vegetate, a somewhat smaller area in which they may vegetate as well as ripen and spawn their sperm and eggs (an area in which the sexual products may ripen but are not spawned may probably occur in certain species), and an even smaller area, in which not only the vegetating, ripening, and spawning but also a successful development of the embryos and larvae may take place.

In addition to the temperature, the food-conditions may also contribute to determine the area of distribution. A species living under temperature conditions which allow the ripening, spawning, and a successful development of the early cleaving stages has afterwards to pass through the critical stage in which the planktotrophic larvae are forced to feed on the plankton. Let us imagine that the species in question has a boreal or southern distribution. In our seas such a species will often find its most optimal conditions for ripening, spawning, and cleaving in the coastal zones of areas with stabilised water masses. Owing to this stabilisation the surface water will be warmer in the summer, but in such a stabilised area the nutritive salts required for the production of the phytoplankton are only carried to the surface in small quantities. Precisely on this account, an area with optimal temperatures for the ripening, spawning, and early development has such small quantities of food for the planktotrophic larvae that most of them will starve and perish. In such areas the nutritive salts present in the uppermost water layers will often be sufficient for a short flourishing of the phytoplankton, which allows a planktotrophic development during a short time only within the period in which the temperature conditions for breeding are optimal. Under such conditions a stock of adults will soon be selected which will start its full spawning during the short period in which the temperature as well as the food conditions are favourable. Such a population will accordingly only breed during a minor part of the period during which the temperature is above the "breeding point". Similar conditions are known for the larvae from several areas of the Danish waters, e. g. the Isefjord.

C. Other spawning inducements.

ORTON (1920, p. 361) states as a main result of his discussion "that sea-temperature must be the influence of paramount importance controlling breeding in marine animals under normal biological conditions". In so far as the conditions found in high-arctic East Greenlandic fjord areas may be regarded as "normal", I am able to give a few examples of cases in which the temperature is without any influence at all as a direct inducer of spawning in marine invertebrates. In each month throughout the year 10—70 vertical plankton hauls were taken from a fixed station in the middle part of the fjords, and the plankton was examined alive immediately after having been collected. The larvae of *Mya truncata* and *Saxicava arctica* are abundant in the plankton during the actual summer season, while they are absent during the winter time. Thus their larval occurrence shows a pronounced rhytm, and the breeding in the summer seems to suggest the temperature as the inducer. However, the first distinct breeding sets in early in May (Thorson 1936), and as late as May 23th the temperatures at the station in question were: At the surface —1.59° C.; at 5 m —1.44° C.; at 10 m —1.51° C. and at 50 m —1.69° C. (Ussing 1938), i. e. the same temperatures as were found in January and during the spring. In June the melting ice forms a brackish water layer on the surface, which kills all animals along the coasts down to depths of 3 to 5 m and stabilises the water masses. The water below the brackish layer, i. e. the layer in which *Mya* and *Saxicava* are most abundant, has therefore still negative temperature. In July, when the larval number is at its maximum, the temperatures are positive (at the surface up to 8° to 12° C.), a fact which does not help to explain that the breeding in *Mya* and *Saxicava*, though distinctly limited to the summer season, sets in on a large scale much earlier than the rise of the temperature. Quite similar conditions seem to prevail in the same area for *Pectinaria granulata* and *Harmothoë imbricata* (Thorson 1936, p. 86).

It is, however, a matter of fact that spawning on a large scale in these species sets in simultaneously with a sudden and heavy increase of the phytoplankton in the East Greenland fjords. It seems natural, therefore, to assume that there is a connection between the quantity of phytoplankton and the breeding season e. g. in the Lamellibranchs mentioned above. Also the observations of Marshall, Nicolls and Orr (1934) on the breeding of *Calanus finmarchicus*, of Steemann Nielsen (1937, p. 3) on the production of Zooplankton in Icelandic fjords, and of Einarsson on north Atlantic *Euphausiacea* (1945, pp. 132—34, with discussion) seem to point in the same direction. This conjecture is further supported by the observations of Miyazaki (1938), who at Japan induced spawning in males of *Ostrea gigas* by adding an extract of the green algae *Ulva pertusa* and species of *Enteromorpha* to the water. The same author has tried several other spawning stimuli, but all without success, and mentions that the extract of 1 mgr wet leaf of *Ulva* is sufficient to induce spawning. The active substance is soluble in the water and tolerates boiling for 30 to 40 minutes without losing its activity. Thus it is not excluded that an increase in the stock of phytoplankton may induce spawning in marine invertebrates. There seems also to be a possibility that the temperature and the phytoplankton maxima may act together as inducements to spawning. The lunar periodicity in spawning within several marine invertebrates seems to occur during a period in which the temperatures are constantly favourable for ripening and spawning. Nevertheless the spawning is rhytmic during this period, and it seems likely that besides the temperature one or more further stimuli may act as inducers of spawning. Amirthalingam (1928) in his detailed discussion of the lunar periodicity mentions observations which seem to show a certain lunar periodicity also in the phytoplankton, and if so it cannot be excluded that the rhytmic spawnings in the invertebrates are caused by such fluctuations. However, these reflectations are mere conjectures, and our present knowledge does not warrant any decisive conclusions on this point. The problems seem nevertheless to be exceedingly interesting and of great significance, and regular continuous observations would, no doubt, be very valuable.

If, however, the production of phytoplankton may act as a spawning stimulus in marine invertebrates, this will be a source of new problems of a wide range for the marine biologists. Miyazaki's experiment mentioned above was carried out on a Lamellibranch, and it is a well known fact that the cleaving and early development in Lamellibranchs takes place very quickly. Shelled, free-swimming veligers are developed in *Ostrea virginica* 52 hours after fertilisation at 18°—$21^1/_2$° C., Galtsoff), in *Gryphaea angulata* 24 hours after fertilisation at 20°—$23^1/_2$° C. (Amemiya 1926), in *Tapes pullastra* 48 hours after fertilisation (Ashworth 1905), and in *Pholas truncata* (North American species) already a few hours after fertilisation (Sigerfoos 1895). Several other examples are known. This means that a phytoplankton maximum which induces spawning in a stock of Lamellibranchs may already a few days later serve as food for the fry which originates from this spawning — a chance which may be of fundamental value to the larvae, provided that the phytoplankton organisms are of such a size that the larvae are able to devour them. If the same phytoplankton maximum causes a spawning in the Echinoderms, Polychaetes, and Gastropods also, conditions will be quite different. The Echinoderm embryos take often up to a week after fertilisation to reach the planktotrophic larval stage, most embryos of Polychaetes and Gastropods are imbedded in gelatinous masses or capsules, from which planktotrophic larvae hatch about two weeks after fertilisation. While the Lamellibranch larvae may feed on the phytoplankton which has induced themselves to be spawned, the larvae of Echinoderms (when reaching the stage of feeding), Polychaetes, and Gastropods (when hatching a week to a fortnight later) will probably find the phytoplankton maximum in decrease, if it has not totally disappeared. Hence, it is of the greatest importance to learn whether phytoplankton is of any value as a spawning stimulus under natural conditions, and if so, whether the Lamellibranchs are more sensitive to such a stimulus than the other groups of marine invertebrates.

3. Conditions Influencing the Length of the Breeding Season.

Ealier in this paper it has been pointed out that the length of the breeding season varies considerably from species to species (p. 400). Some of the species have a very short, others a very long breeding season, and others again a moderately long season.

Among the Danish species with a short spawning season is *Arenicola marina*, which according to the literature performs the whole process of spawning within two days once a year (Pirlot 1933). *Amphiura filiformis* is known to spawn all the eggs contained in a female in a single spawning (Mortensen 1920). Owing to the uniform and abundant occurrence of this species over wide areas of the bottom it is probable that spawning will set in simultaneously in a large stock of specimens, one specimen inducing spawning in the others. As, further, the occurrence of planktonic larvae of this species is limited to a short period of the year, it seems reasonable to assume a very short and distinct breeding season for *Amphiura* in our seas. Several species of planktonic larvae have similar distinct, limited periods of occurrence in the plankton during which a gradual development from a preponderance of young larvae to a dominance of older larvae may be followed during the collecting of a few main series. This seems to show that nearly all the larvae of these species have been spawned contemporaneously and that no further breeding occurs. Forms which behave like this in the Sound and may therefore be supposed to have one short and distinct breeding season per year are e. g.: *Echinocardium cordatum, Brissopsis lyrifera, Psolus phantapus, ?Mysta barbata, Glycera alba, Magelona papillicornis, Myriochele danielsseni, Pectinaria koreni, Eulimella nitidissima*, and *Natica montagui* (cf. the table on p. 403).

The long spawning seasons may depend on several conditions. In the Sound they may e. g. be due to a great vertical distribution of the species. By a rise of the temperature specimens in shallow water will then be induced to spawn earlier in the summer than those in deeper water, where the rise of the temperature sets in later in the year. Examples are: *Nassa reticulata, Bittium reticulatum, Philine aperta, Acera bullata,* and *Montacuta bidentata,* cf. the table on p. 403. – Long spawning seasons may also be due to different spawning times for younger and older specimens within the parent-stock. This is known e. g. for the Decapods *Leander squilla* and *Carcinus maenas.* In our waterst the older specimens of *Mytilus edulis* seem to breed in spring, while the younger specimens will spawn later in the year (Ad. Jensen & Spärck 1934). At Plymouth *Pomatoceros triqueter, Hydroides norvegica, Filograna implexa,* and *Anomia aculeata* contained ripe sexual products four months after having settled, which yielded up to 100 per cent of embryos when artificially fertilised, and already six weeks after settling the Nudibranchs *Eubranchus* (*Galvina*) *pictus* and *Eubranchus pallidus* (= *exigua*) spawned several egg masses from which young veligers were hatching (Orton 1914). Coe (1933, 1934, 1936), at Massachusetts, found several specimens of *Teredo navalis* which contained ripe sexual products not more than 20 days after settling. Orton (1920) found embryos inside the sponges *Grantia compressa* and *Sycon coronatum* which had settled the same summer. It is evident that stocks of such species spawning in the spring and early summer may produce young which will ripen and spawn later in the same season. — Long spawning seasons may finally be due to the individual specimens spawning several times during a single year, e. g. in several Decapods. Spärck (1920) mentions that specimens of *Mytilus edulis* which shed their eggs in large white clouds (in the Limfjord) contained large numbers of eggs also after the spawning had ceased; this shows that spawning takes place more than once per season in one female. Scott (1901, p. 164) states for *Mytilus edulis* from the Isle of Man "that practically the whole of the reproductive elements were discharged at one emission extending from one to three hours. The same mussel did not again set free any more reproductive elements". Our experience from the Isefjord seems to show that only a single spawning of *Mytilus* occurs per year (cf. the graph on p. 404). Thus the mode of spawning seems to vary from place to place. — Long spawning seasons in the Sound are known for the following species (apart from the species already mentioned): *Harmothoë imbricata, Polydora ciliata* and *Polydora coeca, Capitella capitata, Spirorbis borealis, Lacuna divaricata, Littorina littorea, Retusa umbilicata, Limapontia capitata,* and *Mytilus edulis.* Most of these long breeding seasons have only been traced by studying the occurrence of larvae in our main-series, and from these observations it is hardly possible to find out the mode of spawning of the individual species. For *Spirorbis borealis* it is known that the same animal will produce several generations of eggs and larvae in a single season, and for *Littorina littorea* the main-series have shown that at least two large breedings take place in the Sound during the summer (p. 175). The same seems to be the case in *Mytilus edulis.* Thus in these species there seems to be a certain spawning-rhytm. In *Polydora* the spawning also sets in very distinctly and suddenly, but not at regular intervals. In *Capitella capitata, Lacuna divaricata,* and *Limapontia capitata* spawning seems to take place uniformly and without any rhytm at all. From our main-series, taken at intervals of from two to three weeks, it is impossible to make out whether the rhythmic emissions of eggs are connected with any lunar periodicity. Such lunar periodicities are known from foreign seas in species which are frequent also in the Sound, e. g. *Pecten opercularis* (Amirthalingam 1928), *Mytilus edulis, Macoma baltica, Mya arenaria* (Helen Battle 1932), and *Spirorbis borealis* (Garbarini 1933, 1936). It is impossible to deal more closely with these difficult and still unsolved problems here, but it can be stated that the lunar periodicity in the spawning - if there is any at all — is only of little significance in the Sound, and from the Isefjord — an area with a very distinct spawning season — it can be stated that the large spawnings of *Mytilus*, *Littorina*, and *Bittium* as well as *Mya* take only place once a year. Whether this single large spawning has any relation to the lunar phases is, however, unknown. It has been supposed that the lunar phases are of the greatest significance to the animals in areas with a pronounced tide-water, and, as will be known, the tide in the inner Danish waters is inconsiderable.

4. Species with more than one Type of Reproduction.

The fact that several species of marine invertebrates may reproduce in more than one way, is no doubt of fundamental value to them, as in this way they attain an adaptability which makes them able to take up competition over larger areas of the seas than species having only one mode of reproduction. The main point, which is of a special ecological interest, is whether the same species may vary its mode of reproduction from a pelagic to a non-pelagic or from a planktotrophic to a lecithotrophic (cf. pp. 432—438) development according to the surrounding conditions, and it seems necessary to summarise a few data on such variations within the different groups of marine invertebrates.

Actinia: Stephenson (1929, p. 159) mentions as a common rule for the British forms that reproduction by eggs and pelagic larvae may occur in all species, but most of these species have one further method of reproduction, which may be asexual (e. g. in *Metridium dianthus* and in several species of *Sagartia*) or sexual (e. g. the brood-protection in *Tealia felina* and *Hormathia digitata*). Brood-protection and asexual reproduction, however, do not seem to occur in one and the same species, and it would seem that each species within the Actinians is rather strictly associated with one single method of reproduction at least within a large geographical area. There are, however, some exceptions; thus *Metridium dianthus* is known to reproduce both asexually and by eggs and pelagic larvae in the Danish waters, and this is probably also the case with the species *Sagartia lacerata*.

Sponges. Asexual reproduction (mainly by gemmulae) is known to occur in the same species as reproduce by eggs and pelagic larvae. The *Cornacuspongidae* may reproduce by pelagic, asexual gemmula-larvae and by egg-larvae, which, when swimming in the water, are so similar mutually that they can hardly by distinguished from each other (H. J. Wilson 1894). Trégouboff (1942) mentions for larvae of *Tetractinellidae* found in plankton off Villefrance that it cannot be decided whether they originate from eggs or gemmulae.

Echinoderms: In the Danish Echinoderms asexual reproduction seems only to occur as regeneration (e. g. in *Asterias rubens*), and is thus of little significance. It can be stated that no Danish Echinoderm has normally more than one mode of reproduction at its disposal (see, however, Mortensen's remarks (1921, p. 243) on *Asterias mülleri—Asterias groenlandica*). *Henricia sanguinolenta*, which is normally known as a brood-protecting species, has now and then been found not to protect the larvae, which will then float about suspended in the water mass. Under such conditions the larvae have a chance to contribute to the dispersion of the species — a chance which is much reduced when the embryos are protected by the mother animal. The pelagic larvae are, however, of precisely the same type as those protected by the mother.

Polychaetes: A large number of species are known to reproduce asexually as well as sexually. This is known e. g. in *Syllidae*, *Chaetopteridae*, *Cirratulidae*, *Sabellidae*, and *Serpulidae*, but also forms which only reproduce by sperm and eggs have often different modes of development at their disposal. The Polychaetes occupy an exceptional position within the larger groups of marine invertebrates on account of their ability to change their mode of reproduction according to the surrounding conditions. Thus, according to the literature several species living in the Sound are able to change their mode of sexual reproduction. A few characteristic examples are:

Nereis dumerili: Four modes of sexual reproduction are known, including viviparity, and non-pelagic and pelagic larval developments. The individual specimen is able to reproduce in an atoquous way with non-pelagic larvae, and — half a year later — in an epitoquous way with pelagic larvae (HEMPELMANN 1911).

Nereis pelagica: Non-pelagic larval development at Cherbourgh (HERPIN 1925), pelagic larval life (18 days) at Plymouth (WILSON 1932 a).

Harmothoë imbricata: Brood-protection in Arctic seas (IZUKA 1912, THORSON 1936), free eggs and larvae in Danish seas (cf. this paper pp. 46—48).

Spio filicornis: In the same population pelagic larvae are found in spring and non-pelagic embryos, which feed on nurse eggs, in late summer (MESNIL & CAULLERY 1917).

Pygospio elegans: Probably pelagic larvae in spring, and non-pelagic embryos, which feed on nurse eggs, in late summer (SÖDERSTRÖM 1920). Recent Danish investigations (cf. pp. 83—88) seem to show that the species is able to reproduce with larvae of nearly all types from entirely non-pelagic to such with a long pelagic life varying with the areas in which they live and with the seasons of the year.

Cirratulus cirratus: Brood-protection at the Falklands (FAUVEL 1916 a) and gelatinous spawns with non-pelagic development in northern seas (CUNNINGHAM & RAMAGE 1888).

Dodecaceria concharum: Three types of sexual reproduction, all of them non-pelagic. Further, two modes of asexual reproduction are known (MESNIL & CAULLERY 1898 a, and 1898 b).

Pomatoceros triqueter: Normally oviparous, with a very reduced pelagic larval stage (VON DRASCHKE 1884), occasionally viviparous with a non-pelagic development (GRAVIER 1923, p. 218).

Confer also the varying egg-sizes of *Terebellides strømi*, *Nicolea zostericola*, and *Ampharete grubei* mentioned in this paper p. 125, 126 and 121 respectively.

Placophora: The individual species seems to have only one type of reproduction at its disposal. In *Chiton cinereus* (cf. pp. 160—161) the mode of oviposition may vary from brood-protection, through batches adhering to a substratum, to eggs shed freely in the water, but the egg-size seems to be the same in all the cases and the embryos will always hatch in the same stage of development.

Prosobranchs: Normally one mode of reproduction in the individual species. Exceptions in the Danish seas: *Natica catena* may probably have a pelagic or non-pelagic development according to the number of nurse-eggs at the disposal of each embryo (cf. pp. 220—222). The non-pelagic development in *Lunatia pallida* may probably be changed by twin-formation into a pelagic one (cf. pp. 215—216). *Lacuna pallidula* has larger eggs and embryos in the Danish waters than off France although the development is non-pelagic in both localities (cf. pp. 168—170). *Brachystomia rissoides* has extremely varying egg-sizes in different localities, even within neighbouring areas (cf. pp. 204—205).

Opisthobranchs: Not a single case is known within this group in which a species has more than one method of reproduction at its disposal.

Lamellibranchs: The individual species seem to have only one type of reproduction at their disposal, but the variations in the size of prodissoconch I and in the size of the metamorphosing Veligers (cf. p. 279) seem to indicate a certain variation in the length of the larval life within the individual species according to the sea-areas in which they occur. This variation, however, seems never to be so great, that the species will change their principal mode of larval development (e. g. from pelagic to non-pelagic, or from planktotrophic to lecithotrophic).

Cephalopods: The individual species seem only to have one type of reproduction at their disposal.

Crustaceans: In *Balanus balanoides* the normally free-swimming *Nauplia* may, under special conditions, be retained in the mother animal until the *Cypris*-stage (S. Runnström 1925). — A few, not Danish, Amphipods (e. g. *Melita pellucida*, cf. Legueux 1926) are known to have different egg sizes in different areas. — The shrimp *Palaemonetes varians* has much larger eggs in fresh water than in the sea (cf. p. 228); *Crangon crangon* has small summer-eggs and large winter-eggs (cf. p. 321). All other Crustaceans seem to have only one mode of reproduction.

The large variability as to the mode of reproduction within a single species seems thus to be a significant factor in the Actinians, Sponges, and especially in the Polychaetes, while it is of little or no value in the Echinoderms, Prosobranchs, Opisthobranchs, Lamellibranchs, and Crustaceans.

5. The Mode of Development of the Embryos.

No connection seems to exist between the mode of oviposition and the mode of development in the marine invertebrates. In the Danish waters viviparity seems to be associated with a non-pelagic development. Exceptions are, however, known from other seas. The Prosobranchs *Planaxis sulcatus* (New Caledonia, Risbec 1935) and *Littorina angulifera* (Bermuda, Lebour 1945) have for instance viviparity succeeded by a pelagic larval stage. In our seas brood-protection may lead to a non-pelagic development (e. g. in *Asterias mülleri, Exogone gemmifera, Sphaerosyllis tetralix, Nereis dumerili* (nereidogenous form), *Modiolaria discors*, all the Isopoda and Amphipoda), as well as to a long pelagic larval life (e. g. in *Crepidula fornicata* and *Ostrea edulis, Montacuta bidentata* and *M. ferruginosa, Pholas, Teredo, Harmothoë, Polydora, Pygospio, Capitella*, and most *Decapoda*). Finally, our species of *Spirorbis* have brood-protection combined with a shortened pelagic life.

Also when the eggs are laid freely in capsules attached to a substratum the modes of larval development may be very different. A non-pelagic development is found e. g. in *Nucella, Trophon, Sipho, Neptunea*, and *Buccinum*, while pelagic larvae occur in *Littorina littorea, Coecum glabrum*, and in several species of *Rissoa, Nassa, Bela, Philbertia, Mangelia*, etc. Similar conditions are found for eggs laid freely imbedded in gelatinous masses. Thus, e. g. the following species are non-pelagic: *Scoloplos armiger, Cirratulus cirratus, Terebellides strømi, Gibbula tumida, Lacuna pallidula, Littorina obtusata, Hydrobia ventrosa, Brachystomia rissoides, Embletonia pallida*, and *Modiolaria nigra*, while the larvae e. g. of *Phyllodocé groenlandica, Owenia fusiformis, Acmaea testudinalis, Lacuna divaricata, Bittium reticulatum, Triphora perversa, Capulus hungaricus, Actaeon tornatilis, Retusa truncatula, Acera bullata, Philine aperta, Limapontia capitata*, etc. are pelagic. The eggs shed singly and attached separately to a substratum develop into pelagic larvae in *Aporrhais pes pelecani*, while *Macoma calcaria, Astarte borealis, A. montagui*, and *A. elliptica*, which seem to spawn in a similar way, have a non-pelagic development. Nearly all the eggs shed singly and suspended in the water will develop into pelagic larvae with a long planktonic life. Exceptions from the Sound are i. a. *Arenicola marina, Ampharete grubei* and *Thelepus cincinnatus.*

Embryos with a non-pelagic development may feed in several different ways. The majority of them originate from large, yolky eggs sufficiently rich in food to support the whole development to the young bottom stage. Examples are: *Asterias mülleri, Exogone gemmifera, Nicomache lumbricalis, Fabricia dubia, Lacuna pallidula, Littorina obtusata, Trophon truncatus, Modiolaria nigra* and *M. discors, Thyasira flexuosa,* and the species of *Astarte.* Others, normally also with rather yolky eggs, are further surrounded by an egg-white-like substance, which serves as their food, e. g. the Danish Prosobranchs *Lunatia pallida* and *Amauropsis islandica.* Also the gelatinous jelly in which many spawns are imbedded may now and then contain white and serve as food for the young embryos. In all species with these types of feeding the embryonic development seems to be constant, i. e. the embryos leave the egg capsules when reaching a certain size and organisation. Thus, all the hatching young of the same species will normally be in the same stage of development. This, however, is not the case with the method of feeding which is now to be discussed, viz. the feeding on nurse-eggs: Eggs of a size normally found to develop into pelagic larvae are laid several together within a common egg space. Only a few of the eggs develop into embryos, and the rest of the eggs are devoured by the others, which will not hatch until all the nurse-eggs within the egg space have been devoured. Such nurse-eggs, which are especially well known in our large Prosobranchs, have proved to be much more common among marine invertebrates than previously assumed. A review of the literature has shown that feeding on nurse-eggs may be found within the antarctic Crinoids (Mortensen 1920 b), in three antarctic Ophiurans (Mortensen 1921, 1936), in the Polychaetes *Polydora hoplura* (Wilson 1928 a), *Pygospio elegans* (Söderström 1920 and this paper pp. 83—88), and *Spio filicornis* (Mesnil & Caullery 1917), in the Nemertine *Lineus gesserensis-ruber* (Schmidt 1934), and in several Prosobranchs, i. a. *Nucella lapillus, Buccinum, Neptunea, Sipho, Natica catena,* and several foreign species (cf. p. 441). The number of nurse-eggs devoured per embryo varies greatly from species to species. From a few nurse-eggs per embryo in *Natica catena* over an average number of 20—30 nurse-eggs per embryo in *Polydora hoplura* and *Nucella lapillus,* 100 per embryo in *Buccinum undatum,* about 2,500 per embryo in *Neptunea antiqua* and up to 7,000 per embryo in *Sipho islandicus* (Thorson 1935 a), the maximum seems to be reached in the North Atlantic deep-sea species *Volutopsis norvegica,* which uses from 50,000 to 100,000 nurse-eggs as food for a single embryo (Thorson 1940 a).

Also within the individual species the number of nurse-eggs at the disposal of each embryo may vary considerably from place to place or even within a single locality. This is chiefly due to a rather large variability in the number of embryos per egg space. In the North Atlantic Prosobranch *Sipho islandicus* it has been found that capsules with nearly the same quantity of nurse-eggs may contain from one to sixteen embryos. These embryos leave the capsule when they have reached the stage of development which the number of nurse-eggs at their disposal is able to support, and hence it is evident that each of the sixteen embryos contained in a single capsule will hatch in a much younger (though non-pelagic) stage than a single embryo contained in a capsule with plenty of food at its disposal (Thorson 1935 a). Of special interest are these facts in such species in which only a few nurse-eggs are at the disposal of the individual embryo. A good example is furnished by the Prosobranch *Natica catena,* in which the number of embryos varies from 1 to 4 in northern Kattegat, and from 4 to 8 at Heligoland, the number of nurse-eggs per embryo thus being from 5 to 110 at Frederikshavn and from 2 to 27 at Heligoland and farther southwards. In accordance herewith the embryos hatch as non-pelagic young in the Danish seas but may hatch as pelagic larvae in the southern North Sea and the Channel. In other (foreign) Prosobranchs still more intricate conditions are known. The tropical *Planaxis sulcatus* reproduces at New Caledonia without nurse-eggs and with pelagic larvae, in the Iranian Gulf by nurse-eggs and non-pelagic young (THORSON 1940 b). *Thais haemastoma* (= *T. floridana* CONRAD) reproduces in Louisiana without nurse-eggs and with pelagic larvae and in Florida with nurse-eggs and non-pelagic young (BURKENROAD 1931, LAMY 1928).

It was mentioned above that the types of non-pelagic development normally show very constant features for a species as to the size and organisation of its hatching young. Only the nurse-egg method may give rise to such varying conditions that one and the same species may reproduce with pelagic larvae or with non-pelagic young, varying according to the locality.

In addition to the nurse-egg method only one other type of embryonic development, viz. the formation of twin-embryos, seems to cause a variation from pelagic to non-pelagic larvae in the same species of Prosobranch. In the Nudibranchs such twin-embryos are rather frequently found within a single egg membrane, but as the twin-embryos as well as the embryos laid singly here have the same quantity of food at their disposal, viz. the content of yolk within the egg cell proper, they will all hatch in the same stage of organisation (VESTERGAARD & THORSON 1938). In *Lunatia pallida*, however, twin-embryos have been observed in all the egg spaces in a single egg mass from the Sound, while several other egg masses from the same area had never more than one embryo per egg space (cf. pp. 220—22, fig. 132). As the twins in such an egg space have to feed on half the quantity of white of that normally at the disposal of each embryo, it seems probable that they may hatch as pelagic veligers and not, as normally, as crawling young.

The paper by ERIK RASMUSSEN just published (1944) seems to show that the Prosobranch *Brachystomia rissoides* may vary its egg size from locality to locality. Thus the egg size and larval development in this species mentioned by PELSENEER (1911) from France results in a totally non-pelagic development, while the eggs found in the Isefjord (Denmark) and the Sound are much smaller and hatch as veligers, which are able to swim in the water though apparently for a short time only (cf. pp. 204 -206). In Roskildefjord (brackish water) the same species reproduces by eggs even larger than those found near France and the embryos hatch in a totally non-pelagic stage of development (cf. p. 206).

6. Types of Pelagic Larvae.

The pelagic larvae constitute the majority of all the larval invertebrates in the Danish seas. Within the species from the Sound in which the mode of larval development is known they constitute about 89 per cent of the Echinoderms, 70 per cent of the Polychaetes, 66 per cent of the Prosobranchs, 92 per cent of the Tectibranchs and Ascoglossids, and 82 per cent of the Lamellibranchs, i. e. on an average 80 per cent of all the invertebrate larvae within these large groups known from the area in question. Ecologically, however, these larvae may be divided into three distinct groups according to the degree in which they depend on the plankton as a source of food. Larvae which feed on phytoplankton, and larvae which, though swimming in the plankton, feed on their own contents of yolk, belong to two different "systems", and several of the factors regulating one of these types are without any importance for the other. These two extremes among the pelagic larvae are further connected with a third larval type, viz. larvae which feed on the plankton for a very short time only. As these three types of larvae have quite different qualifications, and as precisely the pelagic larval stage is the most critical stage during the whole development of most invertebrates, it seems reasonable to discuss their types and chances in detail.

A. Planktotrophic Larvae with a Long Pelagic Life.

This group comprises on an average about 63 per cent of all the Echinoderms, Polychaetes, Prosobranchs, Tectibranchs, and Lamellibranchs in the Sound the development of which is known, and thus represents the dominating larval type in the plankton. The pelagic stage may last from one week to 2 or 3 months (cf. pp. 451—457). As is well known, the larvae of the different larger groups show quite different features, and the shape and organisation which make them fit for a pelagic life, show numbers of variations from group to group. The older larvae of the Polychaetes, and all the pelagic larvae of the Prosobranchs and Lamellibranchs show external features and an organisation very similar to those of the parent animals. The Polychaete *Nectochaeta* is slender, with bristles, cirri, eyes, etc., like the adults. The Lamellibranch larvae have the same two valves as are characteristic of adult Lamellibranchs, the Prosobranchs have similar twined shells as are found in the parents, and so on. The only differences are that the larvae are provided with organs which enable them to swim and float in the water, e. g. bands or tufts of cilia and the provisional bristles in Polychaete larvae and the velum in Prosobranch and Lamellibranch larvae. The *Trochophora*-stages of the Polychaetes are somewhat more different from their adults, but have already the mouth and the intestine which will also function in the adults. The larval Echinoderms, however, do not show the slightest similarity to their parents, from which they are so different that they were described by earlier zoologists as new unknown organisms, viz. "plutei", and referred to a special group far from the Echinoderms. The gap between the larval stage and the adult stage in the Echinoderms is thus much larger than between the corresponding stages in the Polychaetes, Prosobranchs, and Lamellibranchs.

It has been pointed out elsewhere (pp. 395—396) in this paper that the Echinoderm larvae and the young Polychaete larvae with their rather slow locomotion and with their entirely naked surface exposed to the water seem to be much more sensitive to changes in the salinity and to attacks by Infusorians etc., than e. g. the Lamellibranch and Gastropod larvae, which — withdrawn in their shells — are extremely well protected. Exact experiments to investigate these reactions and their significance are highly desirable but not available at present.

Also as to the mode of feeding different types can be distinguished among the planktotrophic larvae with a long pelagic life, viz.

Nanno- and Ultra-plankton feeders.
Microplankton feeders.
Carnivorous larvae.

The claims of these three groups to the plankton as a source of food will be dealt with in detail on pp. 446—450; here only a few features will be discussed.

Apart from the *Decapod* larvae and probably those of *Magelona* which feed exclusively on animal food, nearly all the pelagic larvae of bottom invertebrates in the Sound which take their food from the plankton are able to feed exclusively on Nanno- and Ultra-plankton. Also such larvae as may live on *Chaetoceras, Coscinodiscus*, and other microplankton animals, viz.

larvae of *Polydora, Glycera* and *Nephthys*, and some of the larvae which are able to live on animal food, viz. *Polydora, Nephthys, Chaetopterus* and *Phoronis*, will find sufficient nourishment in the Nanno- and Ultra-plankton if no other food is available. The microplankton feeders and the larvae living on animal food, and which accordingly should be designated as "omnivorous larvae", have thus the chance that they may grow and feed also during periods in which the Nanno- and Ultra-plankton is rare or absent. Thus in a larval maximum during which the supply of food decreases, omnivorous larvae will have by far the best chances in the competition, and will gradually become absolute dominants in the plankton.

SPÄRCK (1926), in a most interesting paper, records a couple of observations which in a remarkable degree seem to support the conjectures put forward above. Water from the Limfjord (N. W. Jutland) containing large numbers of pelagic larvae of oysters and other Lamellibranchs and at the same time a great many larvae of Annelids were led into heated tanks, where the Lamellibranch larvae perished, while tubes of Annelids covered all the tanks. "In the not heated tanks where the temperature was somewhat lower than in the heated (it was here 18°—20° C.) and with the same kind of pelagic larvae in the water, a much greater number of species attached themselves to the stones, shells, etc. laid out in the tank, than was the case in the heated tanks", (viz. *Ascidiella aspersa, Mytilus edulis, Cardium edule, Mya arenaria*, but, as in the heated tanks, Annelids in the absolute majority). SPÄRCK's conclusions (l. c., p. 279) are: "The fact, that although the larvae are present in almost equal numbers there will only be very few *Lamellibranchiata* (and no oysters) at bottom stages, but an overwhelming abundance of *Annelidae*, might seem to indicate that the larvae of *Annelidae* are more easily nourished than those of the *Lamellibranchiata*. This difference appearing the most distinctly at higher temperatures, at which the competition is the hardest, certainly indicates a problem of nourishment. That it should be due to a greater capability in the larvae of *Annelidae* for enduring variations in temperature or such like is highly improbable" (this is supported by observations on oysters). "The great difference having appeared between the larvae of *Annelidae* on one side and of *Lamellibranchiata* on the other side may, therefore, have its very plausible explanation in a supposed difference, as regards the capability of living on a very scanty supply of nourishment". — Considering our knowledge at the time when his paper was written, SPÄRCK (l. c.) was justified in the conclusion quoted above. Our present knowledge, however, enables us to give another explanation of his observations. The species of Annelids which covered the tanks were, according to SPÄRCK (l. c.), *Nereis diversicolor* and *Polydora coeca* (SPÄRCK (1927, p. 49), recording the same experiments in another paper, states that this latter species is *Polydora ciliata*). The larva of *Nereis diversicolor* is now known to be lecithotrophic, i. e. pelagic, but feeding exclusively on its own content of yolk (cf. pp. 436—438), and has thus no "capability of living on a very scanty supply of nourishment", but a capability of feeding without taking any nourishment from the plankton. The larva of *Polydora coeca* (as also that of *P. ciliata*) is known to be omnivorous, i. e. at higher temperatures it is better off in the competition with the Lamellibranch larvae, which are bound to feed on the Ultra-plankton. But under critical conditions, according to our experience from the Sound, the main food of the *Polydora* larvae will, no doubt, be the Lamellibranch larvae themselves. Hence, it is no wonder that the results in the tanks turned out as stated by SPÄRCK. The Lamellibranch larvae perished, partly because the food supply was too small to support their claim at high temperatures, but above all because they have been devoured by their competitors.

An example from the Sound will further illustrate this. In late December, January, and February, when the production of phytoplankton shows an absolute minimum, only three species of larval invertebrates are frequently met with in the plankton, viz. ?*Mysta barbata*, *Mya truncata*, and *Nephthys ciliata*, which all have their maximum occurrence during these three months. ?*Mysta barbata* is lecithotrophic in the larval stage and thus quite independent of the content of food in the plankton. The larva of *Mya truncata* is an "Ultraplankton-feeder" — the only common "Ultraplankton-feeder" during this season —, feeding on the few flagellates and green algae still present. Early in the season the larvae of *Nephthys ciliata* feed on large *Coscinodiscus* (cf. fig. 32 B, C), and later, when *Coscinodiscus* has disappeared, on *Mya* larvae. Under normal conditions (low temperatures) these three stocks of larvae seem to maintain a certain mutual equilibrium, but if the water were heated and the food requirement increased, it can be taken for granted that the Lamellibranch larvae would perish, while the Polychaete larvae would feed on them and survive.

The Decapod larvae, at least in their older stages, seem to live exclusively on animal food (LEBOUR 1933 c). In the Sound the Polychaete *Magelona papillicornis* seems to feed exclusively on Lamellibranch larvae, of which a number of up to six may be found simultaneously in the intestine of a single specimen. The late larvae of *Chaetopterus variopedatus* have been observed eating Planarians and Copepods (ENDERS 1909).

The dominant mode of development in Danish marine invertebrates is, as mentioned above, that of planktotrophic larvae with a long pelagic life. In the arctic and antarctic coastal waters and in the deep sea the pelagic development is nearly or totally suppressed (HESSE 1924, THORSON 1936, with detailed discussions). In the temperate and tropic coastal areas planktotrophic pelagic larval stages seem to play a still greater part than in our seas (cf. e. g. the Prosobranchs in THORSON 1940 b). As precisely these temperate and tropical coastal zones comprise the largest numbers of animal species known from the sea, it can be taken for granted that the planktotrophic pelagic larval development may be regarded as a method exhibited by the majority of all the marine species of invertebrates.

The advantages of this method are evident. The larvae are small, they originate from very small eggs poor in yolk, i. e. they are "cheap" to produce, and the single mother animal can, therefore, produce them on a very large scale. They have a long pelagic life and are thus able to spread far about with the water masses, to settle in new water areas, and when conditions suddenly change, destroying the original animal stock in a certain bottom area, such invading pelagic larvae may have a chance to settle and found new populations. Of all the types of larvae, those of this type are best fit as "conquerors". In years with optimal food conditions they will often settle in large numbers and their young will totally dominate over large areas of the bottom. Adults with this type of larvae will often spawn only when one year old, probably especially owing to the fact that the eggs are "cheap" to produce.—The disadvantages of the method are that the larvae are totally dependent on the food conditions in the plankton, and during their long pelagic life are exposed to voracious enemies (cf. pp. 467—471). The ability of most of these species to spawn in a very young age, and the fact that larvae from other areas may be carried with the currents to localities in which the larval stock has perished, present, however, a good possibility for a stock of bottom animals to "recover" in a few years, also when the local stock of larvae has been reduced by starvation in a single year. (SEGROVE (1941), in his paper on the development of *Pomatoceros* (which reached me as late as January 1946), gives an interesting discussion of the question of a pelagic versus a non-pelagic development in Polychaetes).

In high-arctic seas a pelagic development is suppressed in up to 95 per cent of all the species of marine invertebrates. However, the few species which in spite of the poor conditions are really able to reproduce with planktotrophic pelagic larvae also in high-arctic seas will have a special chance in the competition there, and such forms are among the most dominant animals of the high-arctic coastal zones (e. g. *Strongylocentrotus droebachiensis, Ophiocten sericeum, Mya truncata, Saxicava arctica* etc., cf. THORSON 1936).

In this connection it must be borne in mind that not all the larvae in the plankton may be classified cathegorically within a single of the groups erected here. Thus it has been stated for *Ostrea virginica* (PRYTHERCH 1924) and for *Ostrea gigas* (FUJITA 1934) that feeding on the plankton does not begin until a certain degree of larval development has been reached. These larvae have accordingly at first a lecithotrophic stage, and the length of their planktotrophic larval life is therefore shorter than their pelagic life.

B. Planktotrophic Larvae with a Short Pelagic Life.

Among the adult species of invertebrates from the Sound the development of which is known, larvae of this type are found in 0 per cent of the Echinoderms, 14 per cent of the Polychaetes, 8 per cent of the Prosobranchs, 8 per cent of the Tectibranchs, and 0 per cent of the Lamellibranchs. The average percentage within these larger groups is thus about 6 per cent, i. e. a rather low percentage, and as the stay of the larvae in the plankton is very short, their significance as planktonic larvae is much smaller than indicated by their percentages given above. — Larvae belonging to this type are e. g.:

Polychaetes: *Autolytus prolifer, A. prismaticus, Arenicola marina, Terebellides strømi, Serpula vermicularis, Miroserpula inflata* (fig. 77), *Filograna implexa, Spirorbis borealis, S. granulatus,* and *S. spirillum.*

Prosobranchs: *Acmaea testudinalis* (fig. 88), *Gibbula cineraria, Hydrobia ulvae* (fig. 104), *Turritella communis,* and *Bela trevelyana* (fig. 140).

Opisthobranchs: The Tectibranch *Acera bullata* (fig. 148) and probably several species of Nudibranch larvae from the Sound (they may, however, be lecithotrophic).

The time spent in the plankton by larvae of this type may probably vary, and definite limits for the length of their pelagic stage cannot be given at present. The figures given below for their stay in the plankton should thus only be regarded as an estimate based upon our experience from the Sound and the available literature. A "common-denominator" for all the larvae of this type is given in the fact that their size and organisation is the same, or very nearly the same, at the moment of hatching and at the moment of settling. Normally the digestive system is fully developed in the hatching larvae, which seem to be able to feed on the plankton. Several species of such larvae are known to do so, but it is likely that under certain conditions larvae of this type may settle without having fed during their short pelagic life.

For most of the Polychaetes belonging to this larval type it seems probable that the planktonic stage lasts for a few hours only. The observations on the above-mentioned species of *Spirorbis* seem to show that hatching takes place during the night and that the larvae settle already before daybreak (cf. p. 137). Their pelagic stage only serves to find a suitable substratum (stones, algae) in the nearest vicinity. However, during these few hours of pelagic life the larvae are able to spread rather far about. Experiments with *Pomatoceros triqueter* near Ven showed that larvae of this species may settle in large numbers on our bottle-collectors 2 to $2^1/_2$ m over the bottom though the pelagic life in the Sound seems to be extremely short. The larvae of *Hydroides, Serpula, Miroserpula,* and *Filograna* will probably behave in a similar way. The larvae of *Arenicola marina* (pp. 108—110) and *Terebellides strømi* (pp. 124—125) may be estimated to spend a somewhat longer time — a few days — in a pelagic or semi-pelagic stage, swimming or floating immediately over the bottom. Blegvad's observations (1923) on *Arenicola* larvae 7 days old and still swimming in his aquaria may, however, be due to unfavourable aquarial conditions, e. g. the lack of a suitable substratum. — The pelagic life of *Hydrobia ulvae, Turritella communis,* and *Bela trevelyana* seems to be still longer, probably up to a week, and here there is hardly any doubt that the larvae feed regularly on the plankton. For most Nudibranch larvae it can be stated that no, or only a very slight growth takes place in the plankton in spite of the well developed digestive system and though some of them have been observed with ultra-plankton in their stomachs. (They thus differ from the Tectibranch larvae, which during their pelagic life feed and grow vigorously in a degree similar to that of the Prosobranchs). The time spent in the planktonic stage by the Nudibranch larvae may probably vary considerably from species to species, and within the individual species also according to temperature, substratum, etc. Allen & Nelson (1911) kept larvae of *Archidoris tuberculata* in aquaria with a *Pleurococcus*-culture for 60 to 70 days. The larvae then died without metamorphosing or settling on the bottom. When compared with the later results of Wilson (1932 b, 1937) and Day & Wilson (1934) for Polychaete larvae, it seems reasonable to suppose that the lack of a suitable substratum is the true reason of this prolonged larval life under laboratory conditions. Stud. mag. Erik Rasmussen has kindly informed me that larvae of *Eubranchus pallidus* kept in aquaria were able to swim about for a month, but during the last time all the swimming larvae were defective and none of them reached the stage of metamorphosis. It seems not reasonable that such small larvae, quite transparent when hatching and apparently without the smallest grains of yolk left to support their future development, will normally spend a month or more in the plankton. As, further, Orton (1914 b) found, at Plymouth, that the present species (synonym of *Galvina exigua*) may grow from veligers to ripe specimens, which spawn egg masses from which the larvae hatch — all this within a space of 6 weeks at the most, it can be taken for granted that a species with such a high metabolism will not spend a larval stage of one month under natural conditions without growing. In *Embletonia pallida* (which has a larval shell and an organisation very similar to those of *Eubranchus* and all the *Tergipedidae, Flabellinidae,* and *Dendronotidae,* cf. pp. 268—271), Erik Rasmussen (1944) has observed that the larvae hatch from their egg mass without any pelagic stage. The pelagic larval stage in nature must therefore be supposed to be short, probably often nearly suppressed, within the Nudibranchs, but definite data are not available.

Summarising the main results for the larval types in question it can be stated that in planktotrophic larvae with a short pelagic life feeding on the plankton is of secondary importance, while the spreading of the larval stock seems to be the main object. The pelagic life is normally short, and always with a very slight growth, or with no growth at all. Laboratory experiments seem to show that the adaptability of the larvae to unfavourable conditions is much greater than might be expected in such small larvae without any supply of yolk in the hatching stage and with no growth in the plankton.

C. Lecithotrophic Pelagic Larvae.

In the Sound this type of larval development seems to occur in all the *Spongia,* in several *Actinia,* in 15 per cent of the Echinoderms, in about 7 per cent of the Polychaetes and about 6 or 7 per cent of the Lamellibranchs, and probably in most species of *Chitonidae,* whereas the type is hitherto unknown for all the Danish marine Gastropods. The larvae in question originate in most cases from rather large yolky eggs, which develop into pelagic larvae of a clumsy shape, rather unfit for active locomotion and often carried nearly passively about by the currents in the water masses. They take no food from the plankton, but feed exclusively on the content of yolk within the egg cell from which they originate.

Examples of such larvae from the Sound are the Anthozoans *Alcyonium digitatum*, *Bolocera tuediae*, and *Tealia felina coriacea* (fig. 6), the Echinoderms *Solaster endeca*, *S. papposus*, *Psolus phantapus* (fig. 192), and, occasionally, *Henricia sanguinolenta*, the Polychaetes *Nereis diversicolor* (fig. 30), ?*Mysta barbata* (fig. 62), *Capitella capitata* (fig. 60), *Notomastus latericeus*, and *Artacama proboscidea* (fig. 73), the Nemertines *Cephalothrix linearis*, *Cephalothrix rufifrons* (cf. J. E. Smith 1935), *Oerstedia dorsalis*, and *Malacobdella grossa*, the Lamellibranchs ?*Nucula tenuis*, *Nucula nitida*, and *N. nucleus*, and, as mentioned above, probably several Chitonid larvae.

The lecithotrophic pelagic larvae seem to be absent from the arctic and antarctic coastal waters and probably also from the deep sea. Apart from these areas with their very extreme conditions they are known from nearly all oceans. As this type of larvae has hitherto been overlooked as regards its ecological significance, a few foreign examples will be mentioned here to show its wide distribution.

Anthozoans: *Pachycerianthus multiplicatus* (Bohuslän, Nyholm 1943, p. 223), *Edwardsia beautempi* (France, Wietrzykowski 1910, 1914).

Echinoderms: *Antedon bifida* (North Sea, Mediterranean, Seeliger 1892), *Antedon petasus* (North Atlantic, Mortensen 1920 a), *Tropiometra carinata* (West India, Mortensen 1920 b), *Ophiura brevispina* (American East coast, Grave 1900, 1916), *Heliocidaris erythrogramma* (Australia, Mortensen 1921), *Cucumaria frondosa* (Norway, subarctic region, J. and S. Runnström 1919), *C. planci* (Mediterranean, Selenka 1876), *C. echinata* (Japan, Ohshima 1918, 1921), *C. normanni* and *C. saxatilis* (British Isles, Newth 1916).

Polychaetes: *Syllis amica* (France, Herpin 1925), *Odontosyllis ctenostoma* (France, Herpin 1925), *Eunice harrassii* (France, Herpin 1925), "*Eunice sp. B*", (India, Aiyar 1933), *Amphitrite ornata* (Woods Hole, Mead 1897), and *Branchiomma vesiculosum* (England, Wilson 1936 c).

Lamellibranchs: *Yoldia limatula* and *Nucula proxima* (Maine, Drew 1899, 1901).

Chitonids: *Chaetopleura apiculata* (Woods Hole, Grave 1922, 1932).

The ecological habits of the lecithotrophic pelagic larvae are very different from those of the planktotrophic larvae with a long pelagic life. The lecithotrophic larvae have the following advantages: They are pelagic, i. e. they may use the water masses to spread over wide areas, but are totally independent of the plankton as a source of food. Their chance of reaching the stage of metamorphosis is therefore much more stable than that of the planktotrophic larvae, which, as mentioned above, will often perish in large numbers during a period with poor food conditions. — The disadvantages of the lecithotrophic larval stages are first of all the large size of the eggs, i. e., the rather small number of eggs per mother animal, and in consequence hereof the failing ability of the relative small stock of larvae to play a part and to take the chance in years with good food conditions.

This mode of development is a typical compromise and therefore lacks the great chances or the great catastrophes which the mode of development of the planktotrophic, pelagic larvae implies. The fact that lecithotrophic larvae seem to be totally absent e. g. in high-arctic seas (Thorson 1936), seems at first to be the opposite of what might be expected. At the outset it would seem likely that precisely this type of larval development, which allows a spreading of the species without the risks connected with a feeding on phytoplankton in these poor regions, would be well fit for the life in arctic seas. The absence of lecithotrophic larvae may probably be due to the fact that the competition in high-artic areas is so keen that no compromise-methods, but only an "either-or", will suffice if a species is to survive. A species living here must either reproduce in a totally non-pelagic way — "the safety first principle" — i. e. a slow method with relatively few young per mother animal, with small chances for spreading, but with good chances for recruiting the stock in a stable way, or it must use the planktotrophic pelagic method with larvae which are able to make the most of the phytoplankton produced during the short summer time, to develop quickly at very low temperatures, and in this very hazardous way to take their chance for a good spatfall.

Of the lecithotrophic larvae, those belonging to *Nucula proxima* (Drew 1901) and to the sponges will stay for a short time only in the plankton (e. g. *Sycon raphanus* (Hammer 1908), *Leucosolenia blanca, Cliona stationis* (Nassonow 1924), *Oscarella lobularis* (Arndt 1928)). It is likely, though not observed with certainty, that several larval Actinians other than those mentioned on p. 437 will behave in a similar way (cf. pp. 27—33). Most of the lecithotrophic larvae of the Polychaetes and Echinoderms seem, however, to stay much longer in the plankton (e. g. 18 days in *Solaster endeca*, cf. p. 345) — probably often just as long as the larvae of the planktotrophic type with a long pelagic life.

7. The "Waste" of Larvae during the Pelagic Life.

A. Fluctuations in the Stock on the Bottom from Year to Year.

The types of larval development described above seem to be more or less suited for a successful competition. A non-pelagic development or — in rare cases — a very rapid planktotrophic pelagic development would thus seem to have the best chances in high-arctic seas (Thorson 1936); in tropic seas planktotrophic, pelagic larvae seem to dominate completely, and in the Danish waters all forms of development seem to occur, with a decided surplus of the planktotrophic, pelagic larvae. The mode of development and the adaptability of the larval stage as a competitor seem to be the essential limiting factors in the distribution of the individual species, and the pronounced cosmopolitic distribution of several Polychaetes in constrast to the other groups of marine invertebrates is most likely explained by the large ability of the Polychaetes to change their mode of reproduction in accordance with the surrounding conditions (cf. pp. 427—429).

If, however, we consider a given area of the sea, it would seem that the mode of reproduction of the individual species of invertebrates living here is well suited for a renewal of the stock on the bottom on a sufficiently large scale to maintain its population. In the Sound, for instance, the stability of the stocks of different bottom invertebrates seems to be nearly the same from year to year over long periods quite independently of the mode of larval development. The modes of development: non-pelagic larvae, planktotrophic larvae with a long or a short pelagic life, and lecithotrophic pelagic larvae, for the species which use them in the Sound and the neighbouring seas seem to serve their purpose, viz. to maintain the population and to ensure the individual species its normal percentual share in the invertebrate stock on the bottom. — These conditions seem only to undergo minor alterations during long periods of years, provided that the hydrographical and ecological conditions within the area remain the same. From the Limfjord, where the fluctuations of the individual species are known to be remarkably great from year to year, large collections of bottom samples have been published from 19 successive years, viz. 1909 to 1927 (Boysen Jensen 1919, and Blegvad 1925, 1928).

In spite of these fluctuations from year to year the average results for a couple of years at the beginning as well as towards the end of this period seem to show nearly the same percentage distribution of the dominating species. The same seems roughly to be the case in the Sound also. Here the percentage frequency of the different species seems to be nearly the same at the present day as fifty years ago. Only for a few soft-bottom animals Brattström (1941) found a gradually increase in number, probably corresponding to an increase of the muddy areas during the last few decades.

These experiences seem to show that each pair of spawning animals will on an average produce precisely that number of eggs and larvae which are sufficient to ensure the growth to maturity and the spawning of another pair of specimens of the next generation. If this claim is not attained during a long period, the stock on the bottom will decrease in number, and if the claim is materially surpassed during a long period, the species will gradually increase in number to finally dominate on the bottom. And, as mentioned above, such changes do not seem to occur within such areas of the sea as have been under scientific observation during a long series of years.

It is, however, a well known fact that in some years extremely large spatfalls of the individual species may suddenly occur. Orton (1937 b) mentions from the British coasts that in good breeding seasons young bottom-stages of *Cardium edule* may settle in suitable localities to the number of up to 100,000 per sq.m. Davis (1923) found, at Dogger Bank, 8250 young of *Spisula subtruncata* per sq.m. Each of four coir ropes exposed in the Baltic water layer in the Sound during 6 weeks in the summer of 1938 was covered with $^{1}/_{4}$ to $^{1}/_{2}$ million of young *Mytilus edulis* per 15 m of the rope. Orton (1932 b) gives, from Plymouth, another example of remarkably large spatfalls in *Mytilus edulis*.

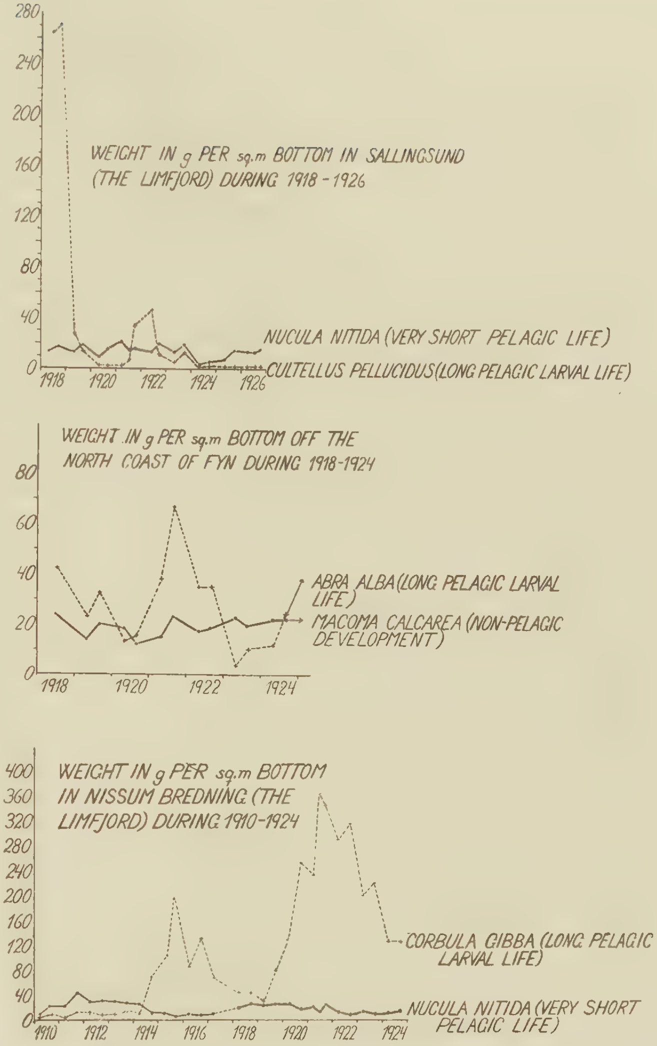


Fig. 199. Curves showing the variations from year to year in a stock of bottom invertebrates recruited partially by larvae with a long planktotrophic pelagic life, partially by larvae with a very short pelagic life or a non-pelagic development. The curves from Sallingsund are drawn on the basis of Blegvad (1928, pp. 40—41), those from Fyn from Blegvad (1925, p. 51, fig. 6), and those from Nissum Bredning from Boysen Jensen (1919, Table III) and Blegvad (1928, pp. 42—43).

The bottom invertebrates, which are subject to these large fluctuations, and which may give such enormous spatfalls, all agree on an essential point: They have planktotrophic larvae with a long pelagic life, i. e. their larvae will flourish or perish according to the prevailing food- (and temperature-) conditions. From the tables of bottom-samples from the Danish waters (Boysen Jensen 1919, Blegvad 1925, 1928) it has been possible to deduce some results which have not hitherto been thrown into relief, though they are very conspicuous when viewed from the point of a pelagic or a non-pelagic development. The authors cited here give the weight in gr per sq.m bottom for the stock of certain bottom invertebrates during several successive years, which allows us to compare species with pronounced planktotrophic larvae and a long pelagic life (e. g. *Cultellus pellucidus, Abra alba, Corbula gibba*) with such species as have a non-pelagic development (*Macoma calcarea*) or have lecithotrophic larvae with a short pelagic life (e. g. *Nucula nitida*), (cf. fig. 199). In all the cases examined it turned out that the stocks of such invertebrates as have a non-pelagic or a shortened lecithotrophic development show only slight variations in weight from year to year, while the stocks of invertebrates which have planktotrophic larvae with a long pelagic life may be subject to very great fluctuations.

There can hardly be any doubt that we are here concerned with one of the main causes of the fluctuations in the quantity of "fish-food", which is of such immense significance to practical marine biology. — The graphs in fig. 199 illustrate also how large a number of young that may at times settle on the bottom, and — in other years — how large a stock of larvae will perish before reaching the bottom stage.

B. The Number of Eggs produced by the Individual Species.

The quantity of eggs and larvae produced by the bottom invertebrates within a given area varies, as mentioned above, considerably from species to species, but in spite of these differences in egg numbers all the species normally occurring here seem to recruite their stock on the bottom on a sufficiently large scale to maintain the population. Hence it may be concluded that species with a larger number of eggs have a larger "waste" of eggs and larvae than those with a few eggs only.

The numbers of eggs and embryos produced by a single female during one season are here given for a couple of species occurring in Danish waters.

Less than 100 eggs: *Asterias mülleri* (50 to 110 eggs), *Henricia sanguinolenta, Exogone gemmifera* (38 young per season), and *Sphaerosyllis tetralix* (64 young per season).

A few hundreds of eggs: *Polydora ciliata, Fabricia dubia, Miroserpula inflata, Spirorbis borealis, Littorina saxatilis var. tenebrosa, Hydrobia ventrosa, Natica pallida*, and *Palaemonetes varians microgenitor* (100—450 eggs).

A few thousands of eggs: *Scoloplos armiger* (3,000—4,500 eggs), *Amphiura filiformis* (probably about 5,000 eggs, a figure which will very likely apply to most other Danish Ophiurans. Verbal information from Dr. Th. Mortensen), *Chiton cinereus* (Clark 1855), *Alloteuthis subulata* (1,000 to 1,500 eggs), *Leander adspersus* (300 to 2,500 eggs per female per year), and *Nephrops norvegicus* (1,000—5,000 eggs).

Several thousands of eggs: *Chaetopterus variopedatus, Phyllodoce groenlandica, Littorina littorea* (about 10,000 eggs = 5,000 egg capsules per female per season), *Crangon crangon* (10,000—35,000 eggs per year), *Carcinus maenas* (up to 185,000 eggs), *Homarus vulgaris* (12,000—15,000 eggs), *Eupagurus bernhardus* (12,000—15,000 eggs), and *Solaster endeca* (about 3,000 eggs in the main spawning and several spawnings per week).

Millions of eggs: *Asterias rubens* (more than $2^1/_2$ millions of eggs in a single spawning, Gemmill 1914), *Cerebratulus lacteus* (100 millions of eggs, Coe 1943), *Aplysia punctata* ($3^1/_2$ millions of eggs in a single spawn), *Archidoris tuberculata* (more than 600,000 eggs in a single spawn, Colgan 1914), *Ostrea edulis* (1 million eggs, Korringa 1941, and others), *Mytilus edulis* (5 to 12 millions of eggs during a single act of spawning; large spms. up to 25 millions of eggs, Field 1923, p. 187), and *Cancer pagurus* ($^1/_2$ to 3 millions of eggs per female per spawn, Williamson fide Pearson 1908).

Similar conditions are known for species in other seas; some of them are even still more extreme. In some Lamellibranchs from New Zealand waters, viz. *Condylocardia concentrica* and *C. Sancti-Pauli,* the mother animal contains only one embryo at a time (Lamy 1928b). The Californian Chitonid *Ischnochiton magdalenensis* may deposit about 200,000 eggs in a single ovulation (Grave 1922). In the starfish *Luidia ciliaris* (North Sea) a ripe female contains at least 200 millions of eggs (Mortensen 1913), the Echinid *Diadema setosum* (Red Sea) produces also millions of eggs per specimen (Mortensen 1938), an oyster, *Ostrea gigas*, spawns about 55 millions of eggs at a time (Galtsoff 1930), and the American oyster (*Ostrea virginica*) produces 100 to 500 millions of eggs per female per year (Needler 1932, Prytherch 1934 b). The most surprising figures known so far are probably those given for the Californian sea-hare *Tethys* (*Aplysia*) *californica*, in which a single specimen within a period of less than five months spawned about 480 millions of eggs, all developing into larvae. This species, as is commonly the case in Opisthobranchs, is hermaphroditic, i. e. all the specimens lay eggs, and the only claim that can be made to these 480 millions of larvae (probably far more larvae are produced during the whole life of an adult animal) in order that the population can be maintained is, thus, that one of the larvae will reach the stage of fertility and spawning! (McGinitie 1934, 1935). Spärck's estimate (1927, p. 54), that only one larva per million of *Ostrea edulis* reached the sedentary stage in the Limfjord in 1914, which was a year with especially favourable breeding conditions, is in good agreement with these figures.

This enormous waste of pelagic larvae is further illustrated by species whose embryos feed on nurse-eggs. From foreign seas we know species (e. g. *Planaxis sulcatus,* Thorson 1940 b, and *Thais floridana,* Burkenroad 1931, Lamy 1928) in which all the eggs develop into pelagic Veligers in one locality, while in another place most of the eggs serve as food for a few embryos. In all the cases hitherto examined these nurse-eggs have an egg size corresponding to that of other eggs which develop into pelagic larvae (hitherto unpublished), and it seems likely that in previous times with more favourable food conditions in the plankton the "nurse-egg feeders" developed all their eggs as pelagic larvae, like the recent time species mentioned above which change from pelagic larvae to nurse-eggs according to the surrounding conditions. If, therefore, at the present day a species reproduces by nurse-eggs instead of by pelagic larvae, it must be supposed that this method is at present most favourable if the population is to be maintained, i. e. the number of nurse-eggs spent per embryo must be smaller than the number of larvae lost if all the eggs had developed in a pelagic way. As it is known that such species may use from 50,000 to 100,000 nurse-eggs to feed a single embryo (e. g. in the North-Atlantic Prosobranch *Volutopsis norvegica,* Thorson 1940 a), it seems likely that the waste during a pelagic life would have been still larger, i. e. that less than 0.001 per cent of the larvae would have survived.

In nature it seems very difficult to obtain reliable figures for the "waste" of larvae within a single species. The statements concerning the stages of development during which the most considerable waste takes place have hitherto been mere suggestions. For many reasons, however, it seems absolutely most likely that the largest waste takes place during the pelagic stage. The immense numbers of eggs spawned by species with this mode of development in contrast to the small egg numbers in species with a non-pelagic development supports this conjecture, and so do also the graphs from Danish waters given in fig. 199.

From the facts stated above it seems possible to outline a method which — when used by future investigators — will give a rather reliable estimate of the size of the waste in planktotrophic pelagic larvae compared with that in species with a non-pelagic development. Examples: In the Sound three species of *Littorina* are of common occurrence, viz. *L. littorea* (planktotrophic larvae with a long pelagic life), *L. obtusata* (non-pelagic development; young hatch from gelatinous egg masses adhering to algae), and *L. saxatilis* (viviparity; young hatch in the crawling stage). As the adults of all three species live under very similar conditions, it seems likely that their young, on reaching the free crawling stage on the bottom, will have equally good chances for their future development. The number of eggs spawned per female in each species seems therefore to be in direct relation to the mode of development of the embryos. Observations on the number of eggs spawned (in *L. littorea* and *L. obtusata*) or young hatched (in *L. saxatilis*) during a year, based upon a sufficiently large number of females, will show the spawning intensity necessary for each species to maintain its population. The egg number in the pelagic *L. littorea* compared with that of the two non-pelagic species will show the percentage of larvae lost during the pelagic stage, etc. — *Nereis pelagica* has planktotrophic pelagic larvae in several places, while *Nereis diversicolor* has lecithotrophic pelagic larvae. The number of eggs spawned by a couple of females of these two species during a year will permit a comparison between the waste of planktotrophic and of lecithotrophic larvae. — *Lunatia pallida* has a non-pelagic development, while *Lunatia nitida* has planktotrophic larvae with a long pelagic life. — *Hydrobia ulvae* has planktotrophic larvae with a short pelagic life, *H. ventrosa* has non-pelagic larvae hatching from the egg capsules in the crawling stage, and *H. jenkinsi*, finally, is viviparous and non-pelagic, and they all live in the same areas, e. g. in the south harbour of Copenhagen, etc.

Such examples will, no doubt, occur within any large area of the sea, and an investigator familar with the local fauna and the mode of reproduction in a larger number of species will have good chances of choosing for his observations a series of species within the same genus but with different modes of development. Observations on the "spawning intensity" in such series seem to me to be the most easy method by which we can gain relatively safe information about the waste associated with the different modes of development. But also for such species as are the only representatives of their genus within an area, reliable observations on their "spawning intensity" will be of the greatest value. Several scientists have observed spawning in marine invertebrates without calculating the number of eggs shed, and without stating whether or not the animal in question extruded all its eggs in a single spawning, and precisely such observations from a number of different species and from different localities are absolutely necessary before we can sketch the first rough outlines of these interesting problems.

A few quite theoretical examples from the Sound will serve to show the difficulty of such matters dealing with the "spawning intensity" and the waste of larvae. At first a comparison between different Prosobranchs from the Sound will be made. The volumes given here should only be regarded as the results of very rough calculations to give the order of magnitude. *Littorina littorea* (height of shell 20 mm) has a volume of about 2200 cmm. The small species *Aclis minor* (height of shell 4 mm) has a volume of about 7 cmm, the volume thus being 300 times smaller than that of *Littorina littorea*. The ovary and the gonoduct seem to constitute nearly the same percentage of the total volume of most Prosobranchs. It must therefore be supposed that the ovary in *Aclis* will also be about 300 times smaller than that of *Littorina*. The direct relations between the size of the ovary and the quantity of eggs produced are well known for several Gastropods, in which the young specimens spawn smaller quantities and the older specimens larger quantities of eggs. It seems likely, therefore, that also the number of eggs produced by *Littorina littorea* will on an average be 300 times as large as in *Aclis*. In both species the hatching larvae are of nearly the same volume, viz. 0.002 to 0.003 cmm, which in both species increases from 5 to 7 times during the planktonic feeding stage.

We have here two species of Prosobranchs agreeing on the following points: They live in the same seas; they produce eggs and larvae of the same order of magnitude. The larvae are planktotrophic and pelagic. The increase in volume during the larval life is of the same order of magnitude, and the pelagic life seems, accordingly, to be equally (or nearly equally) long in both species. The spawning seasons: *Littorina* (May to September) and *Aclis* (August to September), are distinct and rather short, although longest in *Littorina*.

Hence it might be supposed that also the waste of larvae were the same in both species. The result arrived at is just the opposite, viz. that *Littorina littorea* will have to produce a quantity of eggs 300 times larger than that of *Aclis* to maintain its population. The explanation that might be sought in the more rapid ripening of the eggs in *Aclis*, which, in connection with a prolonged spawning season would allow the species to make up for a part of the handicap due to its tiny ovaries, would disagree with the limited breeding seasons actually found. We can hardly imagine that animals which feed on Gastropod larvae in the plankton (e. g. young herrings) will distinguish between the larvae of *Aclis* on the one hand and *Littorina* on the other hand, and according to the reflections stated on pp. 446—450 it seems improbable that food conditions which are poor for the larvae of one of these species will prove to be less poor for another species.

At present it seems impossible to explain these problems, and the purpose of the above discussion is only to point out their existence. Several other examples may be mentioned, e. g. within the Echinoderms: *Echinocardium cordatum* (40 mm in longest diameter) has a volume of 16,000 cmm, *Echinocyamus pusillus* (10 mm in longest diameter) only about 250 cmm. Both have planktotrophic larvae with a long pelagic life, the egg size is nearly the same, but according to the rough calculations of their volume given above, the number of eggs per female per year must be estimated at about 60 to 70 times as large in *Echinocardium* as in *Echinocyamus*. The Decapods *Cancer pagurus* (on an average 1,000,000 eggs 320 μ in diam. per female per season) and *Porcellana longicornis* (about 425 eggs, 310 × 400 μ per female per season) give another example of the same phenomenon.

Species with a non-pelagic development may likewise give rise to similar problems. Near Heligoland *Littorina saxatilis* contains up to 900 embryos at the same time per breeding room (Linke 1933 b), while in the Sound the same species (*var. tenebrosa*) only contains one-tenth of this quantity (cf. pp. 170—173). The species seems to breed throughout the year in both localities, and the crawling young hatch in exactly the same stage of development near Heligoland as in the Sound. Thus near Heligoland this species produces apparently ten times as many embryos per female to maintain its population than seems necessary for the stock in the Sound.

All these problems deserve a much more intensive attention on the part of biologists than has hitherto been paid to them.

C. Fertilisation and "Epidemic Spawning".

To understand the conditions which influence the "waste" of marine invertebrates in the interval between spawning and settling it is necessary to regard in detail the different links in this chain of development, and, if possible, to point out their critical phases and the factors to which they are due. The problems of spawning and fertilisation have already been summarised on pp. 417–421, but to this summary may be added the following supplementary remarks together with a discussion of a more theoretical character.

As mentioned on p. 419, several observations seem to indicate that in a stock of marine invertebrates in which sperm and eggs are shed freely in the water, the ripe males will normally spawn before the females, which are induced to spawn by the surrounding "clouds" of sperm. On some occasions it has turned out that ripe females — although under optimal temperatures and food conditions — are unable to spawn when no ripe male is present (*Ostrea virginica*, Galtsoff 1932, 1938 a-b, and the Chitonids *Mopalia lignosa* and *Ischnochiton magdalenensis*, Heath 1905). — Several of these spawning-observations are recorded in papers dealing with embryological details of individual species and accordingly unknown to most marine ecologists. The phenomenon that the males are the first to spawn, thus stimulating the females to shed their eggs, seems, however, to be so common in marine invertebrates of the most different systematic groups that it must be regarded as an ecological rule for species which shed their sexual products freely in the water. From the available literature I am able to quote the following species, which spawn in the above-mentioned way:

Actinians and Ceriantharians: *Sagartia troglodytes* (Nyholm 1943, pp. 172—174); *Cerianthus lloydii* (Nyholm 1943, p. 112); *Pachycerianthus multiplicatus* (Nyholm l. c., p. 149).

Echinoderms: *Antedon bifida* (Seeliger 1892), *Asterias rubens* (Gemmill 1914), *Amphiura filiformis* (Mortensen 1920 a), *Ophiopholis aculeata* (Olsen 1942), other species of Ophiurans (Selenka 1883), various Echinids (O. Hertwig 1890, p. 282), *Holothuria tubulosa* (Selenka 1876), *Holothuria marmorata* (Mortensen 1937, p. 9—10), *Cucumaria frondosa* (J. & S. Runnström 1919), *Leptosynapta inhaerens* (S. Runnström 1927 b).

Gephyreans: *Phascolosoma vulgare* (Gerould 1906).

Polychaetes: *Pionosyllis lamelligera* (Herpin 1923, with discussion), *Eusyllis blomstrandi* (Herpin 1925, p. 148), *Nereis cultrifera* (Herpin 1925), *Eunice harrassi* (Herpin 1924 a), and *Hydroides dianthus* (Hargitt 1910).

Nemerteans: *Cerebratulus sp.* (Coe 1943, p. 203).

Chitonids: *Chiton cinereus* (Hoffmann 1930—31), *Chiton marmoratus* and *Chiton squamosus* (Metcalf 1893), *Ischnochiton magdalenensis* and *Mopalia lignosa* (Heath 1905), and *Chaetopleura apiculata* (Grave 1922, 1932).

Prosobranchs: *Haliotis tuberculata* (Boutan 1892, pp. 522—525), and *Haliotis gigantea* (Murayama 1935).

Lamellibranchs: *Ostrea virginica* (Galtsoff 1932, 1938 a-b), and *Ostrea gigas* (Elsey 1936, fide Galtsoff 1938).

Some of these observations refer to quite natural conditions (*Ischnochiton, Mopalia, Ostrea gigas*), and several of the others seem to be made under conditions as natural as possible. It can hardly be doubted that similar spawning habits have been overlooked or, when observed, not noted for several other species also. Thus, for the Polychaetes *Diopatra sp.*, and *Podarke sp.* it was observed that the spawning suddenly sets in for a whole stock on the bottom ("epidemic spawning", Hargitt 1910), and a similar simultaneous spawning of males and females was observed in the Nemertine *Cerebratulus lacteus* (B. C. Wilson 1900). The only exceptions which are so far known to me, are those of Herpin (1925), who mentions that in *Nicolea zostericola* and *Perinereis marioni* the females may spawn earlier as well as later than the males, and of Wilson (1936 b), who mentions that females of *Audouinia tentaculata* may spawn in culture dishes, and that sperm added afterwards may fertilise the eggs. Hornell (1894,

p. 13—15) observed in a stock of the Polychaete *Branchiomma* (*Sabella*) *vesiculosa* an "epedimic spawning" and watched as the first spawning specimen a female which was later followed by a male. From his paper it cannot be seen, however, whether he has followed the spawning of the stock in question from its actual beginning or has possibly overlooked the first spawning males. GERSCH (1936, pp. 139—141) discusses in detail the spawning of the Prosobranch *Gibbula cineraria*. He denies that the spawning is induced by a male specimen, but admits that the spawning in a population is "epidemic". Thus 62 animals out of 100 spawned within $3^1/_2$ hours after having been transferred to an aquarium with a temperature which was 5° C. higher than that at which they had been kept during 30 days without spawning at all.

Whether the males induce spawning in the females, or either sex is able to induce spawning in the other sex, the ecological result will be the same: an "epidemic spawning" in which eggs and enormous masses of sperm will occur simultaneously within a rather small water area, thus supporting the possibility for a fertilisation of all the eggs spawned. The "waste" of eggs already at the start owing to failing fertilisation seems, therefore, to be extremely slight and may normally hardly be reckoned among the "critical phases" of the larval development.

Dr. TH. MORTENSEN, studying the development of the Echinoderms, has in a most inspiring manner discussed some ecological problems of importance during the pelagic larval development. This author found at Kristineberg (1920 a) that the males of *Amphiura filiformis* may be induced to spawn also if the salinity is too low to activate the sperm, which will accordingly perish without having induced the females to spawn and without having fertilised the eggs. In the papers from 1937 and 1938 MORTENSEN records similar experiences with inactive sperm for different Asteroids, and both MORTENSEN and HÖRSTADIUS (1926) have succeeded in activating such inactive sperm by raising the p_H of the water (NAOH was added). MORTENSEN (1938, p. 11) is of opinion that the main reason of the large number of eggs in opposition to the small number of settling young in several Echinoderms, is that a very great percentage of the eggs fail to be fertilised. The experiences for *Amphiura* seem to show that emission of inactive sperm may take place also in nature, and it seems likely that the failing maximum of Echinoderm larvae in the Sound in the autumn of 1938 was due to such inactive sperm (cf. pp. 380—381). However, the many examples given above of sperm inducing spawning in female Echinoderms render it likely that sperm shed in an inactive state will bring about not only that the eggs fail to be fertilised but that the eggs will not be shed at all. If this is the case, inactive sperm will mean a waste of sperm but not of eggs, which, if retained in the female after the breeding season, will normally be resorbed and used in the growth of the mother animal. Thus the whole breeding will be disturbed, but this gives no explanation of the fact that during another breeding season the females, when actually induced to spawn by active sperm, i. e. with good chances of having all their eggs fertilised, will shed millions of eggs of which only a few will reach the stage of metamorphosis. MORTENSEN (l. c.) mentions the millions of eggs spawned by a single *Diadema* and the 200 millions of eggs contained in a single ripe *Luidia ciliaris*, and tries to explain the great waste by such failing fertilisation.

Hence it must be kept in mind that waste of a similar order of magnitude is known also for other groups of marine invertebrates than the Echinoderms, and among them are groups in which failing fertilisation seems to be excluded because a copulation takes place before spawning. — The maximum number observed so far for marine larvae seem to be those of the hermaphroditic Tectibranch *Tethys californica* (MCGINITIE 1934, 1935), a single ⚥ of which spawns 480 millions of eggs within a period of less than 5 months. In the Echinoderms two adult specimens — a male and a female — are required for each spawn of eggs and larvae, and similarly, one "pair" (= two ⚥⚥) of *Tethys* will produce about 1,000,000,000 eggs! All the Tectibranchs, however, are known to copulate, and for related genera (e. g. *Acera*) it is known that copulation takes place before each spawn is laid. Further it is known for several species of *Aplysia* that all eggs in the egg-strings are fertilised and develop into larvae.

The results arrived at seem to show that failing fertilisation of the eggs, or rather, failing spawning in the females, may occur also under natural conditions, especially in coastal waters in which brackish water may reach the bottom. Taken as a whole, however, the female marine invertebrates seem to have so sensitive reactions to spawning-stimuli that they will spawn at the very moment at which conditions for fertilisation are optimal, i. e. when the females are surrounded by active sperm of their own species. Failing insemination cannot explain the enormous waste found in most marine invertebrates during the development. It seems only to be of little significance, and the quantities of quite young larvae found in the plankton compared with the relative few settling bottom stages seem also to confirm the conjecture that the heavy waste takes place after fertilisation, during the free-swimming pelagic life.

8. The Food Problems of the Pelagic Larvae.

A. The Food Requirements of the Different Groups of Pelagic Larvae.

By far the majority of the bottom animal larvae feed on small phytoplankton organisms. This has been stated from several successful rearing experiments with larvae of Echinoderms, Polychaetes, Prosobranchs, and Lamellibranchs. Such larvae fed up in plunger-jars on a culture of unicellular algae according to the classical methods described by ALLEN & NELSON (1911, cf. also LEBOUR 1933 c), will normally grow well. These authors (l. c. p. 471) point out for larvae which are to be fed up in cultures, that "the food organisms should be small in size, so that the larvae can draw them into the mouth by ciliary currents". When the food particles swallowed by the larva are larger than $^1/_3$ or, at the most, $^1/_2$ of the internal diameter of the mouth, oesophagus, or fore part of the intestine, the free movements of the cilia in this part of the digestive system will be stopped. As, however, no peristaltic movements of the oesophagus or intestine are seen, and as in most species all the food seems to reach the stomach exclusively by ciliary currents, we can give good information as to the maximum size of the phytoplankton organisms eaten by the individual species of larvae from the diameter of their oesophagus. From such measurements compared with our own observations on the food requirements and with the feeding experiments described in the literature the following data have been deduced:

Echinoderm-larvae. Diameter of oesophagus or front part of intestine: 80—100 μ (measurements from figures in MORTENSEN 1931). Theoretical maximum diameter of food particles: 40—50 μ. Effective food known from cultures: small diatoms, unicellular green algae, and small flagellates (size about 4 μ—30 μ).

Polychaete-larvae. Diameter of oesophagus and front part of intestine (measurements based upon larval sketches from the Sound): 50—100 μ (e. g. in *Glycera*, *Spiophanes*, *Nerine*, *Disoma*, *Myriochele*, *Pectinaria*, and smaller larvae of *Terebellidae*) to 110 μ (*Pygospio*, *Polydora*), 150 μ (*Lanice*), 200 μ (*Nephthys*, ?*Genetyllis*, *Phyllodoce*), 250 μ (*Chaetopterus*), and 300 μ (*Magelona*). Theoretical maximum diameter of food: In the first group 25—50 μ, in the second group 55—300 μ (*Nephthys, Magelona, Polydora, Lanice*, etc. are able to widen their pharynx when swallowing large particles). Observations from the Sound, e. g. on *Glycera alba, Harmothoë imbricata, Eteone longa*, and younger larvae of *Pectinaria* showed that the food present in their stomachs belonged to the 10 μ class. WILSON (1936 a) mentions for young larvae of *Pectinaria koreni* that "it seems that diatoms were too large for them" ("diatoms" here = *Nitzschia*, 30 μ long, 3 μ across). Observations on *Polydora* and *Nephthys* show that they are able to feed on large *Chaetoceras* and large *Coscinodiscus* (200 μ in diameter) respectively, and the same applies according to LEBOUR (1922) to the larvae of *Lanice* and some Polynoids. Effective food known from cultures: small diatoms and tiny flagellates (size about 4—30 μ). Also species with large oesophageal-lumina (e. g. *Polydora, Nephthys, Chaetopterus, Lanice* etc.) are able to feed on these tiny organisms, and have, thus, a special chance to act as competitors under good as well as poor food conditions, as they may take in large diatoms or even animal food if necessary.

Phoronis-larvae. May occasionally eat larval bivalves, but normally eat diatoms and peridinians up to 80—90 μ (LEBOUR 1922).

Cyphonautes-larvae. Normally feeding on small diatoms from 6 to 40 μ in diameter (LEBOUR 1922).

Nemertine-larvae. *Pilidium* larvae mainly feed on small Peridinians (size unknown) (LEBOUR 1922).

Prosobranch-larvae. Diameter of oesophagus or front part of intestine (measurements based upon sketches from the Sound): From 10 μ (young larvae of *Littorina* and *Lacuna*) or 20—30 μ (large *Littorina*-larvae) to 60—70 μ (large larvae of *Natica pulchella* and *Bela trevelyana*) and 90—100 μ (large larvae of *Nassa reticulata*). Theoretical maximum diameter of food: 5—45 μ. Effective food known from cultures: small diatoms (size 3 × 30 μ, used for a number of different genera).

Opisthobranch-larvae. Diameter of oesophagus and front part of intestine (sketches from the Sound): 15—30 μ (*Philine aperta, P. scabra, Acera*). Theoretical maximum diameter of food: 5—15 μ. Observations from the Sound on the size of food in the stomach: 2 to 20 μ.

Lamellibranch-larvae. Diameter of oesophagus and front part of intestine (sketches from the Sound): 7—15 μ (larvae in all sizes of *Cardium, Mytilus, Pecten, Montacuta, Saxicava*, and *Mya*, i. e. with very narrow oesophagus). Theoretical maximum diameter of food: 2—8 μ. Effective food known from cultures: small Flagellates and Diatoms (used for several species, LEBOUR 1938 a).

Decapod-larvae. "For rearing the higher *Crustacea* animal food is necessary, and for the crabs it was found that very young molluscs, newly hatched, or developing echinoderms, and annelids a day or two old answered the purpose". (LEBOUR 1933 c, cf. the same author 1927, pp. 797—98, and 1928, p. 511). Larvae of *Galathea* and *Carcinus* may feed on *Coscinodiscus*, those of *Porcellana* and *Calocaris* on *Rhizosolenia*. Larval Decapods may further eat small Diatoms, i. a. *Navicula* and *Paralia*, Coccospheres (LEBOUR 1922, pp. 658—659) and *Nitzschia* (LEBOUR 1928, p. 511).

The data given above can be summarised as follows:

The Decapod larvae and the older larvae of *Magelona* live mostly or exclusively on animal food. A few larval Polychaetes (e. g. *Nephthys, Polydora, Chaetopterus*) live occasionally on animal food. A few Polychaete-larvae (e. g. *Polydora* and *Nephthys* in the Sound, *Lanice* at Plymouth, and *Glycera* and *Chaetosphaera* in Indian seas (cf. AIYAR 1933)) are able to feed on large diatoms, viz. *Chaetoceras* and *Coscinodiscus* up to 200 μ. The rest — by far the majority

of the bottom animal larvae feed on small phytoplankton organisms and so do also occasionally the larvae mentioned above which may feed on large diatoms and animal food. The maximum size of phytoplankton organisms which the larvae are able to swallow is for Lamellibranchs 8 μ, and for Echinoderms, Prosobranchs, Opisthobranchs, and most Polychaetes 50 μ, but culture experiments and observations in the nature have shown that the size of Phytoplankton normally devoured by bottom animal larvae is smaller, viz. from 2 to 30 μ.

B. The Food Value of the Different Phytoplankton Organisms.

Several phytoplankton organisms have been used with success in cultures in which bottom animal larvae were reared, and also from observations in nature a few data are known. A list of such algae (i. a. their size) and the bottom animal larvae which are known to feed on them is given below. According to the terminological discussions of LOHMANN (1911), NAUMANN (1931), and ÅLVIK (1934) I have used the terms: Mikroplankton (average maximum diameter larger than 60 μ), Nannoplankton (average maximum diameter about 25 μ), and Ultraplankton (average maximum diameter about 5 μ). Most of the sizes are taken from the papers of OVE PAULSEN (*Peridinales*), GRAN (*Diatomea*), and LEMMERMANN (*Flagellata, Chlorophycea*) in the "Nordisches Plankton", 1908. The animals mentioned in the list below refer to larvae only.

Mikroplankton:

Peridinians:

Peridinium ovatum (62 × 84 μ) and *Peridinium conicum* (72 × 76 μ) are eaten by larvae of *Phoronis mülleri* (LEBOUR 1922).

Diatoms:

Biddulphia sinensis (individual cells 120—240 μ in diam.). Eaten in nature by Terebellid larvae and *Cyphonautes* (LEBOUR 1922).

Chaetoceras sp. (Large species, forming chains). Serves as food for *Polydora ciliata* and *P. coeca* (observations from the Sound).

Leptocylindrus danicus (stiff chains, 6—11 μ across). Serves as food for *Polydora ciliata* and *P. coeca* (observations from the Sound).

Coscinodiscus excentricus (50 × 90 μ). Eaten in nature by *Cyphonautes*, Terebellid, Spionid, and Polynoid larvae, Cirriped *Nauplia*, *Galathea* larvae, and *Zoëa* of *Carcinus mœnas* (LEBOUR 1922, pp. 658—59).

Coscinodiscus sp. (Large species, up to 200 μ across). Normally serving as food for *Nephthys ciliata* (observation from the Sound), *Glycera sp.* (Indian seas, AIYAR 1933), and *Chaetosphaera sp.* (Indian seas, AIYAR 1933).

Thalassiosira gravida (about 20 μ in longest diameter in the individual cells; often in chains). Used as food for *Nephthys hombergi* (together with *Nitzschia*, WILSON 1936 a), and in several successful rearing experiments at Plymouth, i. a. with larvae of *Nassa reticulata* (together with *Nitzschia*, LEBOUR 1933 c).

Skeletonema costatum (chains, individual cells 7—16 μ across). Eaten by larvae of *Phoronis mülleri*, Polynoid larvae and *Zoëae* of *Carcinus mœnas* (LEBOUR 1922).

Used as food for older larvae of *Chaetopterus variopedatus* (Allen & Nelson 1911), and for larvae of *Nassa reticulata* (together with *Nitzschia*, Lebour 1931 c).

Melosira sp. (chains; individual cells about 10—30 μ across). Used together with small solitary *Chaetoceras sp.* and *Pleurococcacea* as food for *Echinus acutus* (Allen & Nelson 1911).

Nannoplankton:

Diatoms:

Thalassiothrix sp. (small cells measuring 10 × 60 μ). Eaten by *Cyphonautes* and larval Echinoderms (Lebour 1922).

Thalassiosira gravida (chains; single cell 17 × 62 μ). Eaten by Spionid- and Polynoid-larvae (Lebour 1922).

Thalassiosira nordensköldi (chains; single cell 12 × 43 μ). Eaten by *Cyphonautes* (Lebour 1922).

Nitzschia closterium (3 × 30 μ). Used for *Asterias rubens* (Gemmill 1914), *Asterias glacialis* (Mortensen 1913), *Echinus esculentus* and *Psammechinus miliaris* (Allen & Nelson 1911), *Echinocardium cordatum* (McBride 1914), *Nereis pelagica* (Wilson 1932 a), *Nereis agassizi* (Guberlet 1933), *Nephthys hombergi* (together with *Thalassiosira*, Wilson 1936 a), *Liomia medusa* (Wilson 1928 b), *Sabellaria alveolata* (Allen & Nelson 1911), *Polydora ciliata* and *P. hoplura* (Wilson 1928 a), *Audouinia tentaculata* (Wilson 1936 b), *Chaetopterus variopedatus* (Allen & Nelson 1911), *Owenia fusiformis* (Wilson 1932 b), *Acanthochiton discrepans* (together with other small algae, Hammarsten & Runnström 1925), *Mytilus edulis* (Matthews 1913), several different larval Prosobranchs (Lebour 1933 c, 1937 a), Cirriped larvae (Bassindale 1936, p. 61), and young *Zoëa*-larvae of *Pinnotheres* and *Ebalia* (Lebour 1928, p. 511).

Nitzschia sericata (6 × 100 μ). Eaten by *Cyphonautes* (Lebour 1922).

Chaetoceras sp. (Small species, forming no chains). Used with *Melosira sp.* and *Pleurococcacea* in rearing *Echinus acutus* (Allen & Nelson 1911).

Navicula sp. (Small species 15 × 30 μ). Eaten by *Cyphonautes* (Lebour 1922).

Rhizosolenia sp. (Several small species measuring 5 to 32 μ). Eaten by larval Terebellids and larvae of *Porcellana, Calocaris,* and *Ebalia* (Lebour 1922).

"Small diatoms" (exact size unknown). Used for *Cyphonautes* (Lebour 1922, p. 658) and for several species of Lamellibranchs together with small Flagellates (Lebour 1938 a).

"Diatoms" (exact size unknown). Serve as food for *Chaetopterus sp.* (Aiyar 1933).

Ultraplankton:

Peridinians:

Prorocentrum micans (7 × 24 × 40 μ). Eaten by Polynoid larvae (Lebour 1922).

Small Peridinians sp. Eaten by *Pilidium* larvae, Echinoderm larvae and *Cyphonautes* (Lebour 1922).

Chlorococcum submarinum (6—14 μ). Food (together with species of *Chlorella, Carteria, Brachynema, Catella,* and *Synechococcus,* see these) in the Norwegien oyster-polls for larvae of *Ostrea edulis, Tapes aureus, Modiolaria marmorata, Cardium exiguum,*

of the bottom animal larvae feed on small phytoplankton organisms and so do also occasionally the larvae mentioned above which may feed on large diatoms and animal food. The maximum size of phytoplankton organisms which the larvae are able to swallow is for Lamellibranchs 8 μ, and for Echinoderms, Prosobranchs, Opisthobranchs, and most Polychaetes 50 μ, but culture experiments and observations in the nature have shown that the size of Phytoplankton normally devoured by bottom animal larvae is smaller, viz. from 2 to 30 μ.

B. The Food Value of the Different Phytoplankton Organisms.

Several phytoplankton organisms have been used with success in cultures in which bottom animal larvae were reared, and also from observations in nature a few data are known. A list of such algae (i. a. their size) and the bottom animal larvae which are known to feed on them is given below. According to the terminological discussions of Lohmann (1911), Naumann (1931), and Ålvik (1934) I have used the terms: Mikroplankton (average maximum diameter larger than 60 μ), Nannoplankton (average maximum diameter about 25 μ), and Ultraplankton (average maximum diameter about 5 μ). Most of the sizes are taken from the papers of Ove Paulsen (*Peridinales*), Gran (*Diatomea*), and Lemmermann (*Flagellata, Chlorophycea*) in the "Nordisches Plankton", 1908. The animals mentioned in the list below refer to larvae only.

Mikroplankton:

Peridinians:

Peridinium ovatum (62 × 84 μ) and *Peridinium conicum* (72 × 76 μ) are eaten by larvae of *Phoronis mülleri* (Lebour 1922).

Diatoms:

Biddulphia sinensis (individual cells 120—240 μ in diam.). Eaten in nature by Terebellid larvae and *Cyphonautes* (Lebour 1922).

Chaetoceras sp. (Large species, forming chains). Serves as food for *Polydora ciliata* and *P. coeca* (observations from the Sound).

Leptocylindrus danicus (stiff chains, 6—11 μ across). Serves as food for *Polydora ciliata* and *P. coeca* (observations from the Sound).

Coscinodiscus excentricus (50 × 90 μ). Eaten in nature by *Cyphonautes*, Terebellid, Spionid, and Polynoid larvae, Cirriped *Nauplia*, *Galathea* larvae, and *Zoëa* of *Carcinus mœnas* (Lebour 1922, pp. 658—59).

Coscinodiscus sp. (Large species, up to 200 μ across). Normally serving as food for *Nephthys ciliata* (observation from the Sound), *Glycera sp.* (Indian seas, Aiyar 1933), and *Chaetosphaera sp.* (Indian seas, Aiyar 1933).

Thalassiosira gravida (about 20 μ in longest diameter in the individual cells; often in chains). Used as food for *Nephthys hombergi* (together with *Nitzschia*, Wilson 1936 a), and in several successful rearing experiments at Plymouth, i. a. with larvae of *Nassa reticulata* (together with *Nitzschia*, Lebour 1933 c).

Skeletonema costatum (chains, individual cells 7—16 μ across). Eaten by larvae of *Phoronis mülleri*, Polynoid larvae and *Zoëae* of *Carcinus mœnas* (Lebour 1922).

9. The Duration of the Planktotrophic Pelagic Larval Life.

The time required by the planktotrophic larvae for their pelagic development is, of course, of the greatest significance as a factor influencing the waste. It has been shown above (pp. 435—436) that several species have a very short pelagic life, viz. from a few hours to a few days, and the waste during this short stage must be supposed to be rather small. The planktotrophic, pelagic larvae, however, will normally stay in the plankton for a long time, and it is evident that the risk of waste is the greater the longer the critical free-swimming stage is. Hence, for the problems dealt with in the present paper it is of value to make an estimate — based partly on the literature, partly on our own observations — of the length of the pelagic life in the different species.

It is a matter of fact, however, that the larval life may vary considerably within a single species according to the surrounding conditions. Mortensen (1931, p. 23, 1937, p. 32—33, and 1938, p. 9—11) gives striking examples of the variations of the length of the pelagic life in cultures with Echinoderm larvae. The larva of *Tripneustes gratilla* at Mauritius was only about to pass into the second larval stage at an age of 30 days, whereas at Ghardaqa (Red Sea) the same species had just commenced metamorphosis at an age of 18 days. *Echinometra mathæi* took 40 days from fertilisation to metamorphosis in Japan, but passed through the same development in about half that time near the Red Sea. In the Isefjord larvae of *Mytilus edulis* have under natural conditions been found to take about 4 weeks to pass from fertilisation to metamorphosis (hitherto unpublished), while Matthews (1913, 1917) at Plymouth found that the individual larvae of this species were able to swim about in culture dishes from spring to early September. Several other examples are known; cf. e. g. *Littorina littorea* (this paper pp. 175—176), *Eubranchus pallidus* (p. 270), and *Archidoris tuberculata* (p. 436).

Mortensen (1938, pp. 9—11), discussing the duration of the larval life of the Echinoderms, mentions three factors which may influence its length, viz. the temperature, the amount of food, and the presence or absence of a suitable place to settle. To this may be added, according to our most recent knowledge, the presence or absence of certain substances which further the metamorphosis.

The several failures up to the present day to rear certain larvae of marine invertebrates in cultures (cf. the remarks in this paper on *Nephthys hombergi*, *Pectinaria koreni*, *Ensis siliqua*, *Saxicava arctica*, *Odostomia eulimoides*, *Philbertia gracilis*, *Turritella communis*, *Aporrhais pes pelecani*, and several others), and the failures which are very often experienced in rearings of such larvae as may occasionally be reared in cultures, seem to show that conditions in such cultures are still so far from comparing with the natural conditions that the rate of development in such cultures must be regarded as far from optimal. McBride (1914, p. 473) writes that in *Echinus esculentus* "at least six weeks must elapse before the metamorphosis is completed, and under laboratory conditions a period of two months and more is not infrequently required before the imago condition is attained". Tennent (1910, p. 660), rearing *Toxopneustes variegatus* larvae in the laboratory, states that "no matter how great the care taken, there are sufficient circumstances over which we have no control". Our present knowledge of the duration of the pelagic larval life is, however, mainly obtained from such cultures in the laboratories, only a very few of the available observations originating from larvae living under natural conditions. Thus at the outset it seems natural to expect that the results obtained in the laboratory concerning the duration of the larval life will present longer periods than those normally required by the same larvae under natural conditions.

of the bottom animal larvae feed on small phytoplankton organisms and so do also occasionally the larvae mentioned above which may feed on large diatoms and animal food. The maximum size of phytoplankton organisms which the larvae are able to swallow is for Lamellibranchs 8 μ, and for Echinoderms, Prosobranchs, Opisthobranchs, and most Polychaetes 50 μ, but culture experiments and observations in the nature have shown that the size of Phytoplankton normally devoured by bottom animal larvae is smaller, viz. from 2 to 30 μ.

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Coscinodiscus sp. (Large species, up to 200 μ across). Normally serving as food for *Nephthys ciliata* (observation from the Sound), *Glycera sp.* (Indian seas, AIYAR 1933), and *Chaetosphaera sp.* (Indian seas, AIYAR 1933).

Thalassiosira gravida (about 20 μ in longest diameter in the individual cells; often in chains). Used as food for *Nephthys hombergi* (together with *Nitzschia*, WILSON 1936 a), and in several successful rearing experiments at Plymouth, i. a. with larvae of *Nassa reticulata* (together with *Nitzschia*, LEBOUR 1933 c).

Skeletonema costatum (chains, individual cells 7—16 μ across). Eaten by larvae of *Phoronis mülleri*, Polynoid larvae and *Zoëae* of *Carcinus mœnas* (LEBOUR 1922).

Species	Locality	Culture experiments (C.), or observations in nature (N.)	Normal spawning or artificial fertilisation	Temperature	Duration of larval life	Author
Polychaetes:						
Eulalia viridis	Plymouth & Heligoland	C.	normal	?	10—13 days	Meyer 1938
Nereis pelagica	Plymouth	C.	normal	?	18 days	Wilson 1932 a
Scolecolepis fuliginosa	Plymouth	C.	normal	?	35 days	Day 1934
Polydora ciliata	Plymouth	C.	normal	?	6 weeks at least	Wilson 1928 a
Chaetopterus variopedatus	Plymouth	C.	artif.	?	100 days at least	Allen & Nelson 1911
Sabellaria alveolata	Plymouth	C.	artif.	?	6 to 7 weeks	Wilson 1929
Sabellaria spinulosa	Plymouth	C.	artif.	?	over 4 months	Wilson 1929
Owenia fusiformis	Plymouth	C.	artif.	?	27 days	Wilson 1932 b
Capitella capitata	Naples	C.	normal	?	7 days	Eisig 1899
	Plymouth	C.	normal	?	9 days	Day 1937
Echinoderms:						
Asterias rubens	Firth of Clyde	C.	normal	?	7—8 weeks	Gemmill 1914
	Isefjord	N.	normal	?	about 4 weeks	Thorson, unpubl.
Asterias glacialis	Plymouth	C.	artif.	?	$1^{1}/_{2}$ months at least	Mortensen 1913
Ophiothrix fragilis	Plymouth	C.	artif.	?	26 days	McBride 1907
Ophiocomina nigra	Plymouth	C.	artif.	?	35—40 days	Narasimhamurti 1934
Ophiopholis aculeata	Bergen	C.	normal	8° C.	30 days at least	Olsen 1942
Echinus esculentus	Plymouth	C.	artif.	?	2 months at least	McBride 1911
	Plymouth	C.	artif.	?	6 weeks	McBride 1903
Strongylocentrotus droebachiensis	Bergen	C. & N.	artif.	4°—5° C.	about $2^{1}/_{2}$ months	S. Runnström 1927 c
Echinocyamus pusillus	Kristineberg	C.	artif.	?	8 weeks	Théel 1892
Echinocardium cordatum	Firth of Clyde	C.	artif.	?	24—30 days	McBride 1914
Spatangus purpureus	Plymouth	C.	artif.	about 15°-20° C.	3 weeks	Mortensen 1913
Prosobranchs:						
Rissoa membranacea	Plymouth	C.	normal	?	3 weeks or less	Lebour 1934 a
Nassa reticulata	Isefjord	N.	normal	?	2—3 weeks	Thorson, unpubl.
	Plymouth	C.	normal	?	about 2 months	Lebour 1931 c
Nassa incrassata	Plymouth	C.	normal	?	2 months at least	Lebour 1931 c
Littorina littorea	The Sound	N.	normal	?	4—5 weeks	Thorson, unpubl.
	Isefjord	N.	normal	?	about 4 weeks	Thorson, unpubl.
Bittium reticulatum	Isefjord	N.	normal	?	about 3 weeks	Thorson, unpubl.
Lamellibranchs:						
Mytilus edulis	Massachusetts	N.?	normal	less than 20° C.	about 3 weeks	Nelson 1928 a
	Isefjord	N.	normal	?	about 4 weeks	Thorson, unpubl.
Mya arenaria	Massachusetts	N.?	normal	less than 20° C.	about 3 weeks	Nelson 1928 a
	Isefjord	N.	normal	?	about 2 weeks	Thorson, unpubl.
Decapod Crustaceans:						
Crangon crangon	Heligoland	N.	normal	?	about 5 weeks	Ehrenbaum 1890
Leander fabricii	The Limfjord	N.	normal	?	3 to 5 weeks	Mortensen 1897 b
Palaemonetes varians microgenitor	France	N.	normal	?	15 to 33 days	Sollaud 1919
Cancer pagurus	British Isles	N.	normal	?	about 2 months	Pearson 1908
Homarus vulgaris	Scotland	N.	normal	12.5° C.	about 3 weeks	Williamson 1905b

and *Bittium reticulatum* (Ålvik 1934, Gaarder & Spärck 1932, and verbal information from Professor Spärck).

Pleurococcus unicornis (2—5 μ). Used for *Cucumaria saxicola* and *Archidoris tuberculata* (Allen & Nelson 1911).

Pleurococcaceae (3—4 μ). Used as food for *Echinus acutus* (with *Melosira* and small *Chaetoceras*, Allen & Nelson 1911), and for several Lamellibranchs, Prosobranchs and Polychaetes ("eine marine Protococcoidee", Kändler 1926).

Chlorella vulgaris (3—5 μ). Used for *Mytilus crassitesta* and several other larval Lamellibranchs (together with zoospores of *Ulva* and minute naviculoid diatoms, Miyazaki 1935).

Chlorella pacifica (size?). Used in rearing of larvae of *Ostrea gigas* through metamorphosis to settlement (Hori 1933).

Chlorella spärcki (2.5—7 μ). Food in the Norwegian oyster-poll's for larvae of *Ostrea edulis* and other larvae (together with *Chlorococcum*, see this, Ålvik 1934).

Chlorella sp. (size?). Food for *Ostrea edulis* (Dodgson 1916—26, 1928) and *Asterias glacialis* (Delage 1904).

Polyblepharidacea (5—6 μ, yellowish-green). Used for *Ostrea edulis,* in which more than 90 $^0/_0$ of the larvae feeding on it were carried through from liberation to settlement (Bruce, Knight, and Parke 1940).

"Unicellular green algae" (5 μ). Observed in large numbers in stomachs of living larvae of *Ophiura robusta* in the Sound on $^{20}/_{6}$-42 (unpublished). — (2—3 μ). Used for *Asterias glacialis* (Delage 1904), and *Ostrea edulis* (Spärck 1927).

Carteria micropapillata (10—20 μ)	Food in Norwegian oyster-polls for larvae of *Ostrea, Tapes, Modiolaria, Cardium,* and *Bittium* (together with *Chlorella* and *Chlorococcum,* see this, Ålvik 1934, Gaarder & Spärck 1932).
Brachynema bacillare (1.2—10 μ)	
Catella rubra 1.5—2.5 μ)	
Synechococcus gaarderi (1.2—2.8 μ)	

Chrysomonadales (3—5 μ, golden-brown). Used for *Ostrea edulis,* in which more than 90 $^0/_0$ of the larvae feeding on it were reared from hatching to the young bottom stage (Bruce, Knight & Parke 1938, 1940).

Pontosphaera huxleyi (size?). Used for *Ostrea virginica* (Amemiya 1926).

"Small flagellates" (*Chilomonas, Chlamydomonas* etc., probably 2—10 μ). Used as food for *Echinus esculentus,* for *Cyphonautes* and Echinoderm-larvae (Lebour 1922), and for young larvae of *Chaetopterus variopedatus* (Allen & Nelson 1911), and, together with small diatoms, for several species of Lamellibranch-larvae (Lebour 1938 a).

"Nude flagellates", used in rearing of larvae of *Ostrea edulis* through metamorphosis to settling (Cole 1939).

These data, which by no means claim to constitute a complete list, provide, however, a sufficiently solid basis to warrant the conclusion that the main part of the food in pelagic bottom animal larvae is constituted by Nannoplankton and Ultraplankton. The experiments of Bruce, Knight & Parke (1940) have shown that different species of Ultraplankton, although of the same size, are of quite different value as food for the same species of larvae, and the experiments from the Norwegian oyster-polls have shown that the whole stock of larvae here, Lamellibranchs as well as Prosobranchs, are able to feed exclusively on Ultraplankton (Gaarder & Spärck 1932).

viz. during the actual breeding season of the species, and at this time of the year the room temperatures in the laboratories were probably also rather high. Hence, a very rough estimate seems to show that in northern seas the pelagic development of summer-breeding species and species breeding in the early autumn will on an average take about three (two to four) weeks.

One of the longest periods for a pelagic development stated in the literature in a larva from the northern seas, viz. $2^1/_2$ months, was found for *Strongylocentrotus droebachiensis*. Sven Runnström's estimate (1927 c) seems to be based partly on laboratory experiments and partly on observations in nature. The cultures were carried out at 4°—5° C., and the natural breeding season is in winter. Thus, the long larval life and the low temperatures seem to be associated here. Similar experiences were made by Fraser (1929) for the winter-spawning Lamellibranch *Paphia*. Here six weeks elapse from the egg is spawned till the larva, now 500 μ long, is ready to settle. Spawning took place in January; on February 7th the smallest planktonic larva measured 300 μ long, and no larvae were observed in the plankton later than February 16th. The largest larva found on this date was 500 μ long and was six weeks old at the most, probably somewhat younger. — As to the Lamellibranch larvae Barker Jørgensen has made an unpublished calculation kindly placed at my disposal, which seems to show an average pelagic life of 3—4 weeks in summer-spawning species and 4—6 weeks in winter-spawning species. His results for the summer spawners seem also to cover other groups than the Lamellibranchs, and the results known for *Strongylocentrotus* and *Paphia* seem to show that the long time spent in the pelagic stage is a common feature for winter-spawning species in the northern seas. A pelagic life of from 1 month up to 2 or even 3 months seems rather probable in winter spawning species.

Some species, however, e. g. *Polydora ciliata* are able to set in with distinct spawnings in summer as well as in winter. Maxima of larvae in this species have been observed in February, i. e. the coldest month of the year, and in August, which is very nearly the warmest month as to the temperature of the water. It must therefore be supposed that the time spent by this species in the pelagic stage may vary within wide limits according to the temperature.

Quite similar durations of the pelagic stage are known from larvae in the Tropics, and it is a very interesting fact that larvae living in seas with higher temperatures seem to require just as long a time for their development as those living in the northern seas. The excellent papers of Dr. Mortensen (1921, 1931, 1937 and 1938) dealing with the development of tropical Echinoderms allow us to prepare a scheme of these which, compared with the northern Echinoderm larvae in the scheme p. 453, shows astonishing similarities as to the length of the pelagic stage.

All the data given in the scheme p. 456 refer to experiments made under laboratory conditions. The terms "25°—30° C." and "30° C." for the experiments of Dr. Mortensen in the Red Sea in 1937 (April to June) and 1938 (July to September) respectively, originate from an estimate (verbal information) made by the late Dr. C. Crossland, the director of the Ghardaqua Laboratory. Dr. Mortensen himself has no observations, but remembers that the temperatures (also the room temperatures) were higher during his stay there in 1938 than in 1937 (verbal information). As, further, Dr. Mortensen informs me that the temperature is higher near the Red Sea than at the Japanese stations, where Onoda (1936) reared his larvae, and as Onoda records a temperature of 25°—27° C. during his experiments, it can be taken for granted that the temperatures from the Red Sea estimated here may be regarded as minimum temperatures for the seasons in question.

Species	Locality	Normal spawning or artificial fertilisation	Temperature	Duration of pelagic larval life	Author
Asteroids:					
Astropecten aranciacus	Naples	artif.	?	80—100 days	Hörstadius 1939
— *scoparius*	Misaki	artif.	?	19—21 days at least	Mortensen 1921
— *polyacanthus*	Red Sea	artif.	25°—30° C.	3—4 days	Mortensen 1937
— *velitaris*	Red Sea	artif.	25°—30° C.	5—6 days	Mortensen 1937
Asterope carinifera	Red Sea	artif.	25°—30° C.	1 month	Mortensen 1937
Asterina pectinifera	Misaki	normal	?	18 days at least	Mortensen 1921
Archaster typicus	Java Sea	artif.	?	24 days at least	Mortensen 1931
Pentaceraster mammillatus	Red Sea	artif.	30° C.	24 days at least	Mortensen 1938
Luidia savignyi	Red Sea	artif.	30° C.	about 14 days	Mortensen 1938
Linckia multiflora	Red Sea	artif.	30° C.	4 weeks at least	Mortensen 1938
Ophiuroids:					
Ophiothrix triloba	Red Sea	normal	25°—30° C.	40 days at least	Mortensen 1937
— *savignyi*	Red Sea	normal	30° C.	3 weeks	Mortensen 1938
Ophiomaza cacaotica	Red Sea	artif.	25°—30° C.	12—14 days at least	Mortensen 1937
Ophiocoma erinaceus	Red Sea	normal	25°—30° C.	1 month at least	Mortensen 1937
— *scolopendrina*	Red Sea	normal	25°—30° C.	6 weeks at least	Mortensen 1937
— *lineolata*	Red Sea	normal	25°—30° C.	1 month at least	Mortensen 1937
Ophionereis squamulosa	Panama	normal	?	6 days	Mortensen 1921
Echinoids:					
Eucidaris metularia	Red Sea	artif.	25°—30° C.	4 weeks at least	Mortensen 1937
Prionocidaris baculosa	Red Sea	artif.	30° C.	1 month	Mortensen 1938
Diadema setosum	Red Sea	artif.	25°—30° C.	6 weeks	Mortensen 1937
	Java Sea	artif.	?	nearly 2 months	Mortensen 1931
Nudechinus gravieri	Red Sea	artif.	25°—30° C.	15 days at least	Mortensen 1937
Tripneustes esculentus	Panama	artif.	?	22 days at least	Mortensen 1921
Tripneustes gratilla	Mauritius	artif.	?	38 days at least	Mortensen 1931
	Red Sea	artif.	25°—30° C.	18 days	Mortensen 1937
Lytechinus variegatus	Panama	artif.	?	16 days at least	Mortensen 1921
Toxopneustes pileosus	Mauritius	artif.	?	5 weeks or more	Mortensen 1931
	Japan	artif.	25°—27° C.	20 days	Onoda 1936
Temnopleurus toreumaticus	Japan	artif.	25°—27° C.	about 25 days	Onoda 1936
Mespilia globulus	Japan	artif.	25°—27° C.	20 days	Onoda 1936
Echinometra mathæi	Red Sea	artif.	25°—30° C.	18 days at least	Mortensen 1937
	Japan	artif.	25°—27° C.	40 days	Onoda 1936
Echinometra lucuntur	Panama	artif.	?	19 days	Mortensen 1921
Heterocentrotus mammillatus	Red Sea	artif.	25°—30° C.	40 days	Mortensen 1937
Evechinus chloroticus	New Zealand	artif.	?	5—6 weeks	Mortensen 1921
Heliocidaris tuberculata	Misaki	artif.	?	5—6 weeks	Mortensen 1921
Astriclypeus manni	Misaki	artif.	?	13 days	Mortensen 1921
Echinobrissus recens	New Zealand	artif.	?	15 days at least	Mortensen 1921
Laganum depressum	Red Sea	artif.	30° C.	14 days	Mortensen 1938
Echinodiscus auritus	Red Sea	artif.	30° C.	14 days	Mortensen 1938
Holothurioids:					
Synaptula vittata	Red Sea	normal	30° C.	14 days	Mortensen 1938
Stichopus variegatus	Red Sea	normal	25°—30° C.	about 40 days	Mortensen 1937
Actinopyga serratidens	Red Sea	normal	25°—30° C.	nearly 4 weeks	Mortensen 1937
Holothuria arenicola var.	Red Sea	normal	25°—30° C.	4 weeks	Mortensen 1937
— *impatiens*	Red Sea	normal	30° C.	about 14 days	Mortensen 1938
— *difficilis*	Red Sea	normal	30° C.	about 10 days	Mortensen 1938

These similarities in the duration of the pelagic stage in northern and tropical Echinoderm larvae are also conspicuous within the individual genera. The northern *Ophiothrix fragilis* (Plymouth) had 26 days in the pelagic stage, the tropical species *Ophiothrix triloba* and *O. savignyi* (both Red Sea) 40 days and 3 weeks respectively. The northern *Ophiocoma nigra* (Plymouth) spent 35 to 40 days, the tropical *Ophiocoma erinaceus, O. scolopendrina*, and *O. lineolata* more than 1 month, more than 6 weeks, and more than 1 month respectively.

The experiments of Munro Fox (1936, 1939) are in good agreement with the results given above. As regards species of the Echinoderm-genera *Paracentrotus* and *Psammechinus* he shows that at a given temperature the eggs of a southern species will cleave more slowly than those of a northern species of the same genus.

It is a well known fact that the metabolism in marine invertebrates is much higher in arctic species than in boreal and tropical species. Among the Lamellibranchs, for instance, an arctic species may, at 0° C., have an average consumption corresponding to that at about 8° C. in a boreal species, at about 12° C. in a Mediterranean species, and at about 30° C. in a tropical species (Orton 1923, Spärck 1926, 1936 a, Thorson 1936, and unpublished experiments by the present author from the Iranian Gulf). The conditions found here for the Echinoderm larvae seem to be in good harmony with these results and to support them.

10. The Adaptability of Pelagic Larvae to Unfavourable Conditions.

It is a well known fact that the temperature-conditions (cf. pp. 23—25) and the food conditions (cf. pp. 409—412) in the Sound vary considerably during the different seasons of the year. It has further been shown that certain species of larvae, e. g. *Capitella capitata, Limapontia capitata*, and *Zirphaea crispata*, may occur and apparently thrive in the plankton in all the months of the year, while other larvae, for instance those of *Aporrhais pes pelecani, Bittium reticulatum, Nassa reticulata, Acera bullata*, and *Philine aperta*, may occur in the plankton during 8 to 9 months of the year. During these seasons pronounced maximum and minimum conditions for a successful larval development will alternate, and larvae able to tolerate these varying conditions have, no doubt, a surprising adaptability. Examples of such a great adaptability have already been given (cf. pp. 436, 451), and in connection herewith it has been mentioned that the temperature and food conditions may in a decisive way influence the duration of the larval life. The observations, that larvae of *Eubranchus pallidus* may swim about in aquaria for a month, while under natural conditions the same species is able to grow from a veliger to a ripe specimen spawning eggs from which larvae hatch —all within a period of 6 weeks at most (cf. p. 436), and that larvae of *Pomatoceros triqueter* in nature may to all appearance swarm for only a few hours to a few days (cf. p. 134), while larvae of the same species in Plymouth cultures have spent 33 days in a pelagic stage (Allen & Nelson 1911), are likewise good examples.

There is a certain temperature amplitude within which the larvae in the plankton are able to develop but only a much smaller amplitude represents the optimum temperature for their development. At the lowest temperatures within the main amplitude the larvae are probably able to vegetate for a rather long period, however, without showing further signs of development. In a series of very beautiful experiments Sven Runnström (1927 a) has shown that the first cleaving stages of the marine invertebrates are associated with much stricter limits of temperature than are the older larval stages. Thus, the late larvae with their greater eurythermy are able to live and develop in such areas of the seas in which the just fertilised eggs and the early cleaving stages would perish. The limits within which the whole development of the northern marine invertebrates may take place are, however, rather wide. Sven Runnström (l. c.) gives for instance the following temperature amplitudes within which the eggs (and larvae) are able to develop in Norway: *Strongylocentrotus droebachiensis*, *Cucumaria frondosa*, and *Dendronotus arborescens* from -1° to 11° C., *Mytilus edulis*, *Echinus esculentus*, and *Asterias rubens* from 4°—5° to 16° C., *Psammechinus miliaris*, *Echinocardium flavescens*, and *Echinocardium cordatum* from 7°—9° to 22°—23° C., and *Echinocyamus pusillus* from 3° to 28° C. Also Pelseneer (1901) records a series of experiments showing the lethal temperatures for marine larval invertebrates.

All the species examined by S. Runnström — apart from *Cucumaria frondosa* — live in the Sound and belong to 3 distinct types of distribution, viz. arctic-boreal (*Strongylocentrotus*, *Cucumaria*, *Dendronotus*), boreal (*Mytilus*, *Echinus*, *Asterias*), and Mediterranean-boreal (*Psammechinus*, *Echinocyamus*, and both the species of *Echinocardium*), which in Norway have their breeding periods in winter, in spring, and in summer respectively. The seasons in which these species spawn in the Sound seem on an average to have been shifted to later seasons of the year, viz. for the three types of distribution: the spring, the early summer, and the late summer and autumn respectively, but the temperatures found within the water masses in the Sound during the three breeding seasons in question seem all to lie within the requirements of temperature stated by Runnström. The temperature amplitudes found in the Sound during the breeding season of the larvae in question seem on the contrary to be much smaller than those which the larvae are able to endure. Even such larvae as occur in the Sound plankton during all the months of the year may, if they select the right depths of the water column, pass through their development under astonishingly small temperature variations. In the deepest part of the Sound, 25—30 m, the difference between the warmest and the coldest month is only 5° to 7° C. (from 4°—5° to 10°—11° C.), while the amplitudes at depths from 15 to 25 m are 10° and 7.5° C. respectively (Brattström 1941, p. 92 and 95), that is to say smaller amplitudes than the invertebrates hitherto examined are able to endure. At the surface, however, the amplitude for the year is nearly 16° C., but this is without any significance for the present investigation, as all the larvae occurring there belong to summer-spawning species.

The temperature conditions in the Sound vary within limits which may influence the duration of the pelagic development of the marine invertebrates, but during the actual breeding seasons they never seem to surpass the limits which are in themselves lethal to the larvae originating from these breedings.

Several larval invertebrates seem, however, to be very sensitive to sudden changes in the temperature. Allen & Nelson (1911) observed that larvae of *Sabellaria alveolata*, although quite fresh and kept for a long time in the laboratory, suddenly died at a fall of the temperature from 15°—16° C. to 12° and 9° C. Also Hagmeier (1930, p. 475) mentions the sensitiveness of planktonic larvae to changes in the temperature. Spärck (1927, p. 50, 1929, p. 98), however, states that larvae of *Ostrea edulis* endured rather quick cooling from 18°—20° C. to 0° C. and thrived well at the latter temperature for at least 24 hours. They were also able to survive cooling to —2° C. for a short time, and their temperature amplitude is thus at least 22° C., within which they are able to vegetate for a shorter or longer period. However, temperatures of 15° C. or less will prevent a normal development.

The lack of food is probably the reason most frequently presented in explanation of fluctuations in the larval stocks in our seas. Several observations seem to show that a constant supply of food particles is necessary to meet the requirements of the larvae. Spärck (1929) found that the oxygen consumption in larvae of *Ostrea edulis* was much higher than that of the adults, and he has verbally informed me that according to his (unpublished) calculations a larva of *O. edulis* has to consume about 1 million of microorganisms during its pelagic life of one to two weeks in order to complete its development. Mag. sc. ERIK ZEUTHEN, who during the summers of 1943 and 1944 was working with these problems from the Helsingør laboratory as a special part of the present survey, found in a great number of exact measurements that the oxygen consumption in pelagic larvae of marine bottom invertebrates (Polychaetes, Gastropods, Lamellibranchs, Decapods, and Echinoderms) is about 5 to 10 times as high as the consumption in the bottom stages. It was, however, surprising to observe that the oxygen consumption showed all the degrees of a gradual transition from the youngest larval stages to the adult bottom stages, without any remarkable difference in the oxygen consumption, when the larva leaves the plankton and settles on the bottom. This is also the case with such larvae (e. g. *Nassa reticulata*) as from a pure algal diet in the pelagic stage change to a purely carnivorous mode of feeding in the young bottom stages. All these experiments supplemented with new experiments from the summer of 1946 will be published in a special report by ZEUTHEN, who, however, has kindly allowed me to mention his results here.

After this it was to be expected that most pelagic larvae, when developing at the normal temperatures of their breeding season, would starve and perish after only a few hours' lack of food. However, experiments at Helsingør have shown that at least some of the pelagic larval species are able to tolerate the lack of food for a surprisingly long period. On $^{17}/_{9}$-1940, 730 large larvae of *Nassa reticulata* (in the swimming-crawling stage) were separated from a main series (5 vertical hauls from 30—0 m = a water column of 7500 l water sieved by the net) and placed in a small dish with 25 ccm water from a depth of 30 m. The *Nassa* larvae constituted one-fourth of all the larvae of bottom invertebrates in the water column through which the net hauls were made, i. e. in nature they had a water volume of about 1,400,000 c.cm with its content of food organisms at their disposal. In the tiny glass dish they were concentrated within a water volume which was only $^{1}/_{50,000}$ of that in nature, and in which the content of food was accordingly minimal. The larvae were further placed in the laboratory, where the temperature was much higher (16°—18° C.) than in their natural habitat (10°—14° C. at the most), and here they were swimming about vigorously and in good health 5 days later!

A great adaptability of the planktonic larvae and the youngest bottom stages to unfavourable food conditions was further ascertained in a series of experiments carried out on Ven in the summer of 1939:

Vertical plankton hauls from 18—0 m were carefully taken to the laboratory in Dewar's vessels and the whole content of larvae in 4 or 5 vertical hauls was transferred to small or large aquaria respectively. Two aquaria (one large and one small) were filled with surface water, two with 10 m water and two with bottom water (see the scheme on p. 460), and all the aquaria were placed under quite uniform conditions in a shaded place at a room temperature of 17°—20° C., and were, equally aërated, left undisturbed for 6 weeks. Simultaneously with the start of these experiments a series of plankton samples quite similar to those placed in the aquaria and taken in the same locality were examined on the same day, and their contents of larvae noted down. All the plankton samples contained numerous large larvae of *Mytilus edulis* nearly ready to metamorphose together with larvae of several other species. When these experiments were started, bottle-collectors were placed in the sea just where the plankton hauls had been taken. The coir-ropes from the buoys to the anchors in these collectors were thus suspended in the water column at a depth of from 0 to 18 m. Six weeks later the aquaria as well as the bottle-collectors were thoroughly examined, and the animals found in them were counted, measured, and compared. The results for *Mytilus edulis* are given in the scheme below:

Number of vertical hauls	Type of aquarium	Type of water. Salinity	Number of specimens found after experiments	Average length of shells	Largest and smallest specimens found
5	large	surface w. 7.6 $^0/_{00}$	196	460 μ	300—750 μ
4	small	—	51	325 μ	250—400 μ
5	large	10 m w. 14.2 $^0/_{00}$	115	730 μ	450—1100 μ
4	small	—	60	350 μ	250—500 μ
5	large	bottom w. 25.1 $^0/_{00}$	34	585 μ	350—850 μ
4	small	—	59	360 μ	300—500 μ
Experiments in nature		21°—15° C. 10—20 $^0/_{00}$	$^1/_2$-$^1/_4$ million per coir-rope	c. 6000 μ	c. 2000—11000 μ

In all the aquaria the *Mytilus* larvae had metamorphosed or were in the stage of metamorphosis six weeks later. Their size, however, varied considerably. The aquaria with the poorest conditions (small aquaria with surface water) had a stock of young *Mytilus* with shells of an average length of 325 μ (specimens down to 250 μ were found) and showed still remnants of the velum and distinct eye-spots, which is in good agreement with the observations that *Mytilus* larvae in our seas metamorphose at an average length of 300 to 350 μ. The aquaria with the best conditions (10 m water, large aquaria) showed a stock of young with an average length of 730 μ (specimens up to 1100 μ were found), i. e. typical young bottom stages already far from metamorphosis.The free-hanging coir-ropes in the sea exposed for a similar period were covered with young *Mytilus*, which had grown to an average length of the shell of 6000 μ (specimens up to 11,000 μ were found). According to a rough estimate the difference in the average volume for the most slowly developing young in the aquaria and for the stock on the coir-ropes was 1 to 4000 or 5000, although all of them were of the same age! As the temperature conditions were the same in all the aquaria and nearly the same as in the sea, it seems reasonable to ascribe the variations in size and development to differences in the food conditions (and for the surface water probably also to the influence of brackish water). It is an interesting fact, however, that even the smallest bottom stages, which under the poor conditions had hardly passed the larval stage were still alive, crawling vigorously about in the vessels. And *Mytilus edulis* is further a typical summer breeder in the Sound, and in such species a smaller adaptability is to be expected than in larvae which are able to thrive in the plankton during all the months of the year.

11. Problems of Metamorphosis.

A. Phototaxis and Vertical Movements of the Larvae.

The positive or negative reaction of the larvae of bottom invertebrates to light are of the greatest importance for their development and ecology. When analysed, the problems associated with phototaxis prove to be very delicate and difficult. Experiments made by several authors have shown that the positive or negative phototaxis in marine organisms may vary according to the temperature, and that organisms which are photopositive at a faint diffuse daylight will behave photonegatively to direct sunshine, etc. It is impossible to go into these details here (see, however, Loeb 1911, John Runnström 1918, Kalmus 1931, and Fraenkel & Gunn 1940). What is of interest for the present investigation, is only to know the reactions in a couple of larvae belonging to different systematic groups at the mean-temperatures in the sea and at a diffuse daylight of the intensity which they will meet during their normal life in the water masses.

Moore (1909, p. 6), who worked with tow-netting samples placed in glass jars at diffuse daylight as well as at light from a candle on a level with the water, found for all the organisms in the jars that "still the positive ones are near the surface and the negative ones near the bottom". This seems to show, what was to be expected *a priori* and what has later been stated by several authors, that an attraction by the light will cause a crowding near the surface of the water, and that larvae keeping closely to the surface are positive to light. As the aim of the present reflections is to find out whether the pelagic larvae are distributed in different water layers during the different phases of their planktonic life, it is sufficient to state here either that they crowd at the surface or that they are positive to light.

For the Echinoderms, Polychaetes, Nemertines, Prosobranchs, and Crustaceans I have been able to extract from the literature and from my own observations a series of examples of young marine larvae which are known either to crowd at the surface or to be photopositive, viz.:

Echinoderms: larvae of *Luidia sarsi* (Gemmill 1915, p. 577); the Asterids *Astropecten polyacanthus*, *A. velitaris*, and *Asterope carinifera* in the larval stage are "usually keeping close to the surface of the water" (Mortensen 1937). The larvae of the Crinoid *Lamprometra klunzingeri* "are rather strong swimmers and show some positive phototropism" (Mortensen 1937). For *Echinocyamus pusillus* it is stated that fowling detritus may easily be removed from the bottom of a glass jar by means of a siphon "because the larvae as a rule live near the surface or at least at some distance from the bottom" (Théel 1892, p. 5). For the Echinoid *Laganum diplopora* "it was noted that the larvae all kept swimming close to the bottom of the dish, never rising to the surface, as do otherwise as a rule young Echinoderm larvae" (Mortensen 1921, p. 108). Young larvae of *Psolus phantapus* taken from plankton in the Sound and placed in aquaria crowd at the surface (own experience from Ven 1938 and Helsingør 1942).

Polychaetes: Young larvae of *Phyllodoce mucosa* are positive to light (Hagmeier 1930, p. 528), young larvae of *Eteone sp.* swarm at the surface (Willemoës-Suhm 1871), larvae of *Nephthys hombergi* just hatched "swam to the surface" (Fuchs 1911), young larvae of *Lepidonotus sp.* are photopositive (Mead 1897). Larvae of *Polydora* are photopositive (Wilson 1928 a, Spooner 1933), young larvae of *Poecilochaetus serpens* are positive to light (Spooner 1933), and so are young larvae of *Aricia foetida* (Eisig 1914, p. 312) and young larvae of *Capitella capitata* (Eisig 1899). Young larvae of *Spirorbis borealis* swam at the surface (Fewkes 1885), "small Spionid larvae" are photopositive, and "small Polychaete larvae provide further examples of forms which can be strongly photopositive" (Spooner 1933).

Nemertines: *Pilidia* of *Cerebratulus lacteus* are photopositive (C. B. Wilson 1900). Young larvae of *Cephalothrix rufifrons* are positive to light, while older larvae do not "show any reponse, positive or negative, to the stimulus of light" (J. E. Smith 1935, p. 343).

Prosobranchs: Young larvae of *Haliotis gigantea* are photopositive (Murayama 1935).

Young and medium-sized larvae of *Eulimella nitidissima* and *Natica montagui* are photopositive (own observations, cf. pp. 210 and 220).

Crustaceans: Photopositive are: *Balanus balanoides*, nauplia one day old (SPOONER 1933), young larvae of *Crangon crangon* (EHRENBAUM 1890) and of *Palaemonetes sp.* (LYON 1906), larvae of *Pandalus montagui*, *Maia squinado*, *Porcellana sp.* in the first *Zoëa* stage, young larvae of *Carcinus maenas*, larvae of *Pinnotheres maculatus*, *Upogebia sp.*, *Galathea squamifera* larval stages I and II, *Galathea dispersa* larval stages I and II (all from SPOONER 1933).

For by far the majority of the larvae mentioned above it has especially been pointed out that the conditions found refer to the young, newly hatched larvae, and these examples, gathered more or less at random from the literature, seem to show that several — probably most — of the marine, pelagic larvae of bottom invertebrates will rise to the surface immediately after hatching. In the whole literature on planktotrophic larvae with a long pelagic life I have not been able to find a single unimpeachable observation of photonegative young larvae apart from *Laganum diplopora* mentioned as an exception by MORTENSEN. Further it must be mentioned here that careful observations (KORRINGA 1941, pp. 107—110) seem to show indifference to light in pelagic larvae of *Ostrea edulis*.

This reaction, viz. to rise to the surface, seems very fortunate in such young larvae. Thus, far from the bottom and near the food-producing surface layer they may be carried widely about by the water masses, which serve to disperse the species. From this position they will rise and sink in the water according to the varying intensities of light, salinity, and temperature. This reaction depends, no doubt, on a very sensitive mechanism in the larvae.

The pump-series from the Sound (cf. pp. 381—392) showed that several larvae in the Kattegat layer did not pass beyond the limit of the more brackish Baltic water which forms the surface layer in the Sound. The same pump-series, however, showed that by far the majority of the larvae in the Kattegat water had crowded in the uppermost part of this layer, while only a few larvae were found in the layer just above the bottom. This crowding may probably be explained by the fact that the photopositive young larvae move upwards, towards the light, but are prevented from rising higher by the brackish surface layer and the change in the temperature. Our observations supply also several examples of young larvae which crowd at the surface of our plankton dishes as near the light as possible.

In older larvae conditions are quite different. GEMMILL (1920) states for the Actinian *Metridium dianthus* that "older larvae tend to remain at the bottom". MEAD (1897) found for *Lepidonotus sp.* that the young larvae were photopositive, older larvae photonegative. GIARD (1876) showed that young larvae of *Salmacina dysteri* are photopositive, older larvae photonegative, and this is also the case with the larvae of *Notomastus latericeus* (WILSON 1933). Young larvae of *Malacobdella grossa* (HAMMARSTEN 1918) and of *Phoronis mülleri* (DE SELYS LONGCHAMP 1904) swim near the surface, old larvae near the bottom. WELSH (1932) found for the mussel crab *Pinnotheres maculata* that "larvae 30 hours old were less sensitive to light than larvae 15 hours old". Young larvae of *Palaemonetes varians microgenitor* are strongly photopositive, while just metamorphosed bottom-stages are photonegative (SOLLAUD 1921). — Young larvae of *Solaster endeca* swim at the surface; late larvae descend to deeper water layers (GEMMILL 1912). — Also our own investigations give hints in the same direction. In our own glass dishes the oldest larvae are always most closely associated with the bottom and show a pronounced photonegativity (especially observed for *Limapontia capitata*, *Philine aperta* and *Nassa reticulata*).

Only six observations of larvae which are photopositive also in the stage of metamorphosis are known to me from the literature and from my own observations. MORTENSEN mentions, according to CHADWICK (1914, p. 474), "that on certain parts of the coasts of Denmark metamorphosing brachiolariae of *Asterias rubens* may be seen swimming at, or near, the surface of the sea in large numbers during July". In the Danish waters this phenomenon seems to be restricted to areas with a high salinity at the surface (observed by me in the western Limfjord and off Frederikshavn, but not in the Sound, i. e. to localities in which the adults of *A. rubens* have their main occurrence in quite shallow water). SEGROVE (1941) found that the metamorphosing larvae of *Pomatoceros triqueter* in English waters are positively phototactic and settle just below the water line in glass dishes. In England the adults of this species live in the tidal zone, but in the Sound with its brackish surface water the adults live in deeper water, and the larvae, in spite of their positive phototaxis, will hardly pass beyond the upper limit of the Kattegat water. FEWKES (1885) mentions that hatching larvae of *Spirorbis borealis* will swarm at the surface and are able to metamorphose and to secrete their first thin tubes here "until the increasing specific gravity of their bodies sinks them to their future homes". As is well known the adults live on *Fucus* near the surface. SVEN RUNNSTRÖM (1925) found at Bergen that *Cypris* larvae of *Balanus balanoides* were still more photopositive than the *Nauplia* and swam directly at the surface of the water, and he calls the attention to the possible connection between this phenomenon and the nearly exclusive occurrence of the adults in the tidal zone. Observations from the Sound have shown that larvae of *Pygospio elegans* are photopositive even in the oldest planktonic stage, which is in good agreement with the habitat of the adults, viz. near the shore and the surface. SPÄRCK (1920) found in the Limfjord that the young just metamorphosed bottom-stages of *Mytilus edulis* are photopositive. This information seems to me to agree well with the results obtained for *Asterias, Pygospio, Pomatoceros, Spirorbis,* and *Balanus*, as, like these, *Mytilus* is also associated with the tidal zone and with shallow water.

These problems, which deserve a much closer examination from an ecological point of view, are of the greatest importance if we are to understand the conditions about the critical stage of metamorphosis. If the photonegativity is a general feature in older pelagic larvae, this inclination to avoid the light will no doubt be of great value for the larvae in their search for a suitable place to settle and to metamorphose. The photonegative larvae will be "forced" towards the bottom, and swimming along here, they have a good chance of finding the substratum which they prefer for their adult life.

B. Choice of Substratum.

The period when the pelagic larvae are going to metamorphose and settle, e. g. to find a suitable substratum, seems to be one of the most critical phases during the whole larval development. BELDING (1912) points out that the survival of the larvae of *Mya* and *Venus* depends largely upon the character of the mud and sand forming the surface layers of the bottom. NELSON (1928 b, p. 189) states concerning larval Lamellibranchs: "When the time for "settling" arrives the larvae must attach or die" . . . "Since the veligers during their pelagic existence have been distributed widely by currents it follows that for those which through chance happen to "fall upon good ground" there will be many more which through this same chance will "fall by the way side" and be destroyed". . . . "The presence of a suitable substratum is the most important single factor limiting distribution". — These points of view were generally accepted by marine ecologists until a few years ago, being very popular, more especially since they helped us to explain the heavy waste of larvae which actually takes place between fertilisation and metamorphosis. As late as 1937 YONGE accepted this "either-or" in the metamorphosis of two species of *Aporrhais*.

The last few years, however, have given several hints which seem to show that at this point, also, the larvae possess a much more pronounced adaptability than hitherto assumed. MORTENSEN (1921, pp. 105—106) in his great work on Echinoderm larvae briefly mentions an observation which gives the first information about the true conditions. He says: "As metamorphosis" (in larvae of the Echinoid *Mellita sexies-perforata*) "did not proceed further during the next days, I suspected that it was due to the lacking incitement of a natural bottom. Some of the larvae were then transferred to a jar with sand on the bottom, and after a few days these larvae had completed their metamorphosis, while those left in the jar without sand on the bottom showed hardly any further advance in the process of metamorphosis". — These larvae, then, have a certain period during their pelagic life within which they are able to metamorphose (when a suitable substratum is found) or to continue their pelagic life (if such a substratum is absent). As such old larvae nearly ready to metamorphose are normally photonegative, i. e. will swim near the bottom, they have the chance during this period to "test" the bottom at intervals. Carried with the currents they will thus be able to "test" large areas of the bottom within a few days, in which way their chances for selecting a suitable substratum are considerably increased.

In 1934 DAY & WILSON, and in 1932 (b) and 1937 WILSON, have undertaken a series of beautiful experiments in order to clear up these problems in the Polychaete larvae *Scolecolepis fuliginosa*, *Owenia fusiformis*, and *Notomastus latericeus* respectively. Their convincing results showed that larvae ready to metamorphose are able to postpone metamorphosis until a substratum suitable for adult life is reached, meanwhile continuing to swim and grow for a period of several days (*Notomastus*) to several weeks (*Scolecolepis*). Hence, in these forms the choice of a substratum is not entirely due to chance. DAY & WILSON (l. c.) mention that to all appearance a similar postponement may occur in *Polydora hoplura*, *Pomatoceros*, and *Sabellaria*, and add that "worms that have a post-larval pelagic stage in a secreted tube (*Lanice*, *Liomia*, *Arenicola*, *Pectinaria*) will almost certainly be able to live and grow for some time after the stage at which they would normally become planktonic". — Observations from the Sound seem to support this conjecture for *Pectinaria*.

In a main series from Ven, 18—0 m, taken on $^5/_8$-1942, young larvae of *Pectinaria koreni* in stage I, i. e. without a secreted tube and with internal paleae, were abundant, while no larvae in stage II were found. Placed in a 25 ccm Petri dish in the laboratory the sample was inspected on the same evening, but no changes were observed. In the morning of August 7th, i. e. 36 hours after the inspection, three of the larvae were found to be provided with a secreted tube and with external paleae, and another larva with external paleae was about to secrete its tube. In the morning of August 8th a new main series with all the *Pectinaria* larvae still in stage I was taken and transferred to a Petri dish, and here they metamorphosed into stage II with external paleae and secreted tubes within a few hours. Three days later the plankton samples from the Sound still contained only young larvae (stage I) of *Pectinaria koreni*, but our observations have shown that already several days before these larvae were able to metamorphose when they were forced by the conditions (probably the higher temperature and the poor food conditions in the Petri dish) to do so, and will therefore probably also metamorphose when the conditions are favourable, i. e. when a suitable substratum is met with.

But also after having metamorphosed larvae in stage II are able to swim or float in the plankton for a certain period.

Wilson (1937) is of opinion that this ability to choose the right substratum is much more common than hitherto assumed among marine invertebrates, and he mentions the "swimming-crawling stages" in e. g. *Nassa, Philbertia, Rissoa,* and *Natica* stated by Lebour (1931—36) as facts supporting this conjecture. Mortensen (1938) states for the Echinoderms *Prionocidaris baculosa, Fromia ghardaquana,* and *Heterometra savignyi* a similar relation between the duration of the larval life and the presence of a suitable substratum, and Matthews (1917) found for *Alcyonium digitatum* that larvae which normally metamorphosed seven days after fertilisation were able to postpone their metamorphosis for at least 14 days after fertilisation. All these observations give further evidence that the results obtained may be generalised for large groups of larvae.

Also our experiments with bottle-collectors in the Sound (cf. pp. 19—23) seem to support the conjecture that marine bottom invertebrates are able to actively choose their substratum. Vast numbers of metamorphosing larvae and just metamorphosed young in these bottle-collectors have chosen their substrata with an astonishing precision. Metamorphosing stages of *Zirphaea crispata* were found in numbers boring in the cork floats and only there; *Pomatoceros triqueter, Balanus improvisus, Psolus phantapus,* and *Anomia squamula* in metamorphosis were only associated with the smooth surfaces; *Phoronis mülleri, Capitella capitata, Chaetopterus variopedatus,* larval *Terebellidæ,* etc., in all stages of metamorphosis were only found on the oblique glass surfaces covered with a thin layer of mud; larvae and young of *Amphiura, Ophiura, Echinocardium, Myriochele, Onoba, Bela, Philine, Cultellus, Cardium,* etc., crowded exclusively in the layer of soft detritus in the bottle-neck. The detritus layer forming the centre and the bottom of the whole glass-funnel, i. e. the layer in which most of casually settling larvae — if any — would be stored, contained, however, not the slightest traces of such larvae as were abundant on the surrounding substrata. One of the main advantages of the bottle-collector is that it comprises all types of substrata within a small area, thus giving all larvae a fair chance to reach a suitable place for metamorphosis. The surprisingly dense crowding of the different larval types precisely on their typical substratum, however, in spite of the small distances, seems to indicate an active selection of a suitable place for settling.

Hence there are good reasons to believe that several, probably most, pelagic larvae have a certain space of time just before metamorphosis during which they may or may not metamorphose, all according to the presence or absence of a substratum suitable for the young bottom stage. Even if the current along the bottom is slow, for instance $^1/_2$ knot only, a larva ready to metamorphose will have the chance of being carried over rather wide distances within a relatively short space of time, thus in the case outlined above over a distance of about 24 km within 24 hours, i. e. about 170 km per week. And some of these larvae are known to be able to postpone metamorphosis for several weeks. Such larvae ready to metamorphose, forced towards the bottom by their negative phototaxis and testing the bottom at intervals, are carried over areas so large that their chance to find a suitable substratum for settling and metamorphosing seems to be very great. This advantage will probably help the larvae to avoid the huge waste, which would have been inevitable if the metamorphosis — as formerly supposed — took place in mid-water, the young afterwards passively sinking to the bottom without being able to choose or test their substratum or to rise and swim again.

For the realisation of the whole larval ecology it is a very significant point to clear up these problems. The observations of Jägersten on the metamorphosis of *Protodrilus* on different substrata, and those of Allen (1914) and Harvey (1939) on organic substances controlling the growth of some diatoms which have already been mentioned in this paper (p. 17), further serve to demonstrate the subtility of this very interesting crisis within the larval development.

C. Larvae Metamorphosing in Mid-water and afterwards Continuing their Pelagic Life.

Nelson (1928 b) mentions that Lamellibranch larvae which are not able to find a suitable substratum must die, and Mortensen (1938) states that Echinoderm larvae in the same situation will continue to swim about until they die. Thus, to all appearance this is normally the case, but also this rule seems to be less general than previously assumed.

Day (1937, p. 36) found "that the Spionid *Scolecolepis fuliginosa* may, after an abnormally prolonged larval period, actually metamorphose and grow while swimming in a plunger-jar. This observation does not contradict previous experiments (Day & Wilson 1934) on the effect of the substratum on metamorphosis, but shows that in the absence of suitable conditions Polychaete larvae will eventually metamorphose in midwater". Th. C. Nelson (1928 b) mentions that larvae of *Mytilus edulis* form an exception within the Lamellibranch larvae, being able to continue their planktonic life also after a narrow rim of the purple dissoconch shell has been formed, and he has observed "well developed dissoconchs floating freely in the water bearing large bubbles of secreted gas within the branchial chamber".

These are — as far as I know — the only examples recorded in the literature of bottom animal larvae which metamorphose and afterwards continue a pelagic stage for some time.

In an unpublished paper dealing with embryonic whorls dissected out of the adult shells of North Atlantic Tectibranchs Dr. H. Lemche mentions some very interesting observations which he has kindly placed at my disposal: *Diaphana minuta* Brown (= *D. hyalina* Turton, see this paper pp. 251—52) has a wide North Atlantic distribution. The larval development is pelagic, and the oldest pelagic larvae (fig. 147 A-B) have a shell closely resembling the embryonic whorls dissected out of adult Danish shells (fig. 147 G). In marine Gastropods the mode of development is normally known to be constant for the individual species throughout its area of distribution. It is therefore surprising that this species, though reproducing by pelagic larvae, is known in living specimens from the North Atlantic from depths exceeding 1000 m. On examining the apices of specimens from these depths, Dr. Lemche found that the embryonic shells were much larger than in the shallow water specimens, "the difference being that the last larval whorl increases more than else and continues growing for a longer time than usual". Lemche is of opinion, and I can only agree with him, that the deep-water specimens in the North Atlantic originate from drift-larvae which have been carried from the shallow-watered coast areas to the deep-sea, where, in lack of a suitable substratum, they have postponed their metamorphosis and continued their mid-water life till reaching a much larger size and a much later stage than is normal in such species.

Our main series from the Sound, however, contain several examples of such mid-water metamorphoses. — The net hauls forming the basis of our main series are — as mentioned on p. 14 — vertical hauls taken from the bottom to the surface. Hence it may occasionally happen that the net touched the bottom with its upper brim, thus bringing up young bottom stages together with the plankton. Such samples from net hauls which have touched the bottom, will always betray themselves at once when examined in the laboratory, as they are very rich in fæcal pellets, as well as in *Foraminifera*, *Harpacticidae*, *Ostracoda*, and other small bottom forms. Experience has shown that samples from which such large quantities of fæcal pellets and *Foraminifera*, etc., are absent, can with certainty be regarded as "pure plankton samples" without any material from the bottom. — Also such "pure plankton samples" may, however, contain metamorphosed young, which still float in the water masses. Within the Echinoderms this phenomenon seems to be rather common; in the other groups it is rather rare, and as regards a few species, only a single metamorphosed specimen has been found in mid-water during four years' regular collecting. During our investigations such "pelagic bottom stages" were found in:

Echinoderms: *Asterias rubens* (4 specimens known), *Ophiura robusta* (9 specimens from 2 different dates), *Amphiura filiformis* (several specimens from different years and dates), *Echinocyamus pusillus* (5 specimens from 3 different dates), *Echinocardium cordatum* (several specimens from different years and dates), and *Brissopsis lyrifera* (2 specimens from the same date).

Polychaetes: *Phyllodoce groenlandica* (2 specimens from 2 dates), *Harmothoë imbricata* (4 specimens from 3 dates).

Prosobranchs: *Onoba vitrea* (3 specimens from the same date), *Odostomia turrita* (several specimens from different dates), *Odostomia acuta* (1 specimen only), *Turritella communis* (1 specimen only), *Aporrhais pes pelecani* (a few specimens), and *Bela trevelyana* (1 specimen only).

Opisthobranchs: *Actaeon tornatilis* (1 specimen only), *Philine aperta* (a few specimens from a single date), and *Philine punctata* (1 specimen only).

To these may be added the observations mentioned above for *Scolecolepis fuliginosa* and *Mytilus edulis*, and it is seen that this mode of metamorphosis, though not commonly met with, is of a certain significance. If we consider the very small volumes of water sieved by our nets (cf. pp. 370—371), it is obvious that the total water mass of the Sound may contain millions of such "pelagic bottom stages", which thus give the species in question an extra chance for spreading to other areas. How long these young are able to live in the plankton after metamorphosis is unknown, but if such "pelagic bottom stages" are compared with young settled in the bottle-collectors, the maximum age of which is known, it seems likely to assume that they have spent up to one month in the plankton after metamorphosis.

The occurrence or non-occurrence of the Benham-stage in *Arenicola marina* (cf. pp. 108—110) may probably also be explained by the phenomenon mentioned above. In the Sound, where adult individuals of *Arenicola* are abundant, the Benham-stage has never been observed, while such stages are known to be frequent e. g. in North Sea plankton, swimming in the water masses in a gelatinous tube. In the Sound with its relative calm water, where even in the middle part of the waterway the distance to the shore is only a few kilometres, it seems likely that all the larvae will normally find a suitable place in which to settle within a few days. The rough water in the North Sea in connection with the currents and the large distances from the middle part of the sea area to the sandy tidal zones render it probable that several larvae of *Arenicola* may here be carried away from the shallow water areas, where their parents live; they may thus be forced to metamorphose in mid-water, i. e. to pass through a Benham-stage. However, this is only a conjecture, but a closer investigation is not without interest.

12. The Pelagic Larvae and their Enemies.

The data obtained from observations on such phases during the pelagic larval life as have been supposed to be most critical for the larvae indicate such a great adaptability within the larvae that these phases must be regarded as much less critical than hitherto assumed, and accordingly the mortality among the larvae during these phases may be supposed to be much smaller than hitherto believed.

The waste caused by failing fertilisation of the eggs seems to be diminutive. The waste caused by starvation, though considerable, seems likewise to be smaller than might be expected, owing to the ability of most of the larvae to feed on several different Phytoplankton organisms often ranging within rather wide limits of magnitude, and to starve for a couple of days without dying. The adaptability of the larvae to varying temperatures seems also to be much larger than might be expected beforehand. Finally several, probably all the larvae are able to prolong their pelagic life and to postpone their metamorphosis for some days or weeks, which in connection with the photonegativity of the older stages give them good chances for testing the bottom and for finding a substratum suitable for their adult life. Also in this respect the waste previously regarded as enormous seems to be rather small.

According to these observations it might be expected that the total waste in the pelagic bottom animal larvae were much smaller than assumed by earlier authors. However, this is not the case. The waste in the pelagic, planktotrophic stage is for most species of a very large order of magnitude. This is clearly shown by the enormous number of eggs shed and fertilised per each pair of adults with pelagic, planktotrophic larvae as compared with the number of eggs shed by species with a non-pelagic development. — A large waste takes actually place among the pelagic, planktotrophic larvae, but the main conditions causing this waste are probably different from those hitherto regarded as most essential.

It can be taken for granted that, in spite of the adaptability of the larvae also on this point, the presence or absence of food is one of the main factors regulating the development and accordingly responsible for a great percentage of the waste. This assumption is supported by the fact that the poor conditions of the phytoplankton production in high-arctic seas is associated with a fauna of bottom invertebrates in which 95 per cent of all the species have a non-pelagic larval development (Thorson 1936). The much smaller number of eggs spawned by the individual female in species with pelagic lecithotrophic larvae as compared with such with a planktotrophic larval type seems likewise to show that a considerable part of the waste in planktotrophic pelagic larvae is due to starvation. The *Mytilus* experiments (p. 459–460), the tank experiments from the Limfjord (p. 433), and several other observations on the combined food and temperature conditions give evidence of the great part played by the food as a vital factor, though they demonstrate at the same time the adaptability of the larvae to this factor.

The enemies of the pelagic bottom animal larvae have hitherto been too much ignored as a factor responsible for a considerable waste in the planktonic larval stock and our knowledge on this point is still very poor. The compilation below, however, gives in broad features a picture of the large number of animals which feed to some extent or entirely on pelagic bottom animal larvae.

Enemies in the plankton. Several holoplanktonic animals from the Protozoans to the Fishes may feed on pelagic bottom animal larvae. *Noctiluca* has been observed eating larvae of *Ostrea edulis* (Dodgson 1922) and *Ostrea gigas* (Hori & Kusakabe 1926). *Aurelia aurita* has been seen feeding on larvae of *Ostrea edulis* (Orton 1922 b), and *Ctenophora* of the genera *Pleurobrachia* (Kincaid 1915) and *Mnemiopsis* (Nelson 1925 a, b, 1927, 1929) may feed on larvae of *Ostrea virginica*. In the latter case up to 125 oyster larvae were found in the stomodæum of a single Ctenophore and up to 15 Ctenophores were found in one cubic metre of water. Several pelagic Coelenterates of the genera *Steenstrupia, Turris, Rathkea, Obelia, Phialidium, Saphenia, Aurelia* (*Ephyra*-stage), *Pleurobrachia,* and *Beroë* are known to feed occasionally on Annelid larvae (i. a. larval Spionids) and Gastropod larvae and regularly on larvae of several Decapods, e. g. *Porcellana, Gebia, Carcinus, Pandalus, Hippolyte,* and *Crangon* (Lebour 1922).

Certain marine Copepods are known to feed partially on *Nauplia* and other small Copepods (Lebour 1922), and it seems likely that they are able to feed on bottom animal larvae as well.

The principal enemies of the pelagic larvae are probably the fishes. Lebour (1921, 1924 and 1934 a) states that young herrings at Plymouth "up to a length of about 12 mm and just after the yolk-sac had disappeared" feed to a great extent on pelagic larvae of Prosobranchs and Lamellibranchs. "Out of 140 young being examined, 91 had fed on these small gastropods". The same author (1933 e) mentions that small Prosobranch larvae form the chief food of our plankton-eating fishes (herring, pilchard, and sprat) especially in their young stages. Jespersen (1928) mentions that Decapod larvae and *Nauplia* and *Cypris* larvae of Balanids are common in stomachs of young as well as older herrings. Larvae of Polychaetes, Gastropods, and Lamellibranchs are also frequently eaten, but their quantitative significance as food seems to be small. Blegvad (1916, p. 69) found, on examining young of *Belone acus* in the Snekkersten harbour, that they contained Gastropod and Lamellibranch larvae in their stomachs, and such larvae were also found in the stomachs of adult specimens of *Scomber scomber*. Nordgaard (1912, p. 41) found *Mytilus* larvae in the stomachs of sprat.

It seems reasonable to assume that such small pelagic larvae constitute a much greater percentage of the food of pelagic fishes than appears from the available observations. Owing to their tiny size, their fragile structure, and, as regards Echinoderm and Annelid larvae, their rapid dissolution after their death they have undoubtedly often been overlooked in the fish-stomachs examined, embedded as they are in a common mass of larger food-animals. — The large swarms in which young of herring, pilchard, sprat, mackerel, and garfish may occur in our seas make it probable that we are here concerned with one of the principal factors responsible for the enormous waste of the planktonic larvae.

The bottom animal larvae in the plankton may also feed on other pelagic bottom animal larvae. Thus it is known that the larvae of *Nephthys, Polydora,* and *Chaetopterus* and more accidentally those of the Polynoids, *Poecilochaetus,* and *Phoronis mülleri* (Lebour 1922), are carnivorous, feeding partially on larval Lamellibranchs, and that larvae of *Magelona papillicornis* and of Decapod Crustaceans feed mainly or exclusively on animal food, especially on other planktonic larvae. Larval Actinians have been observed eating larvae of *Ostrea gigas* (Hori and Kusakabe 1926). The larvae of *Porcellana, Galathea, Gebia, Axius,* and *Pandalus* are known to feed regularly on larval Echinoderms and larval Molluscs. (Lebour 1922, 1927, pp. 797—98, 1928, pp. 500—511). — The number of for instance Lamellibranch larvae eaten per Decapod *Zoëa* per day is unknown, but the Decapod larvae seem to be very voracious. Remembering the fact that for instance the individual female of *Cancer pagurus* may give birth to 3 million larvae during a single season, all feeding on other pelagic bottom animal larvae, it will be seen that also the tribute taken here must be regarded as considerable.

Enemies on the bottom. Bottom animals, sedentary as well as mobile, may, however, likewise feed on planktonic larvae.

In July 1943 the present author observed in the Isefjord a *Scyphistoma* (probably of *Aurelia aurita*) with a larva of *Nassa reticula* in its stomach. *Alcyonium digitatum* thrives well in aquaria feeding on larvae of *Bothryllus* (Matthews 1917) and is probably also able to feed on other pelagic larvae. In *Virgularia mirabilis* Lamellibranch larvae may be found in abundance in the gastral cavities (Jungersen 1904, p. 50). Blegvad (1914, p. 43) has seen larvae of Prosobranchs and Lamellibranchs in the stomachs of adults of the Actinian *Sagartia viduata*, and Nyholm (1943, p. 224) mentions planktonic larvae and Copepods as food of older larvae of *Sagartia troglodytes*. — Blegvad (1914, p. 43), in the stomach of another Actinian, *Edwardsia chrysanthellum*, observed larval Lamellibranchs with a shell 300 μ long and with distinct eye-spots (probably *Mytilus* larvae). Adult specimens of *Cerianthus lloydi* and *Pachycerianthus multiplicatus* are known to feed on plankton, i. a. Copepods and probably also Polychaete larvae (Nyholm 1943, p. 222).

Adult specimens of *Echinocyamus pusillus* with larval molluscs in their stomachs (Hunt 1925) have been found. — Young crawling bottom stages of *Nassa reticulata* which have lost their velum are able to feed on metamorphosing Lamellibranch larvae (Lebour 1931 c, p. 800).

Blegvad (1914, p. 7—8) mentions adult specimens of *Mytilus edulis* with larval Gastropods and Lamellibranchs in their intestines and adult specimens of *Pecten varius* and *Ostrea edulis* (p. 9) with a few larval Lamellibranchs in their stomachs. Hunt (1925) on various occasions observed Lamellibranch larvae in the intestine of *Pecten opercularis*. Korringa (1941) in the stomachs of adult specimens of *Ostrea edulis* found a few larvae of their own species, and Nelson (1921) mentions that larvae of *Ostrea virginea* may be found in considerable numbers (up to 62 larvae in the stomach of one adult oyster) in stomachs of adults of their own species. — The fact that Lamellibranchs may eat larvae of their own species, on certain occasions even in large numbers, may be explained by the special mode of feeding in these animals, viz. on particulate material and microorganisms suspended in the water respired, and retained during the passage of the water through the gills. Since the gill filter is able to retain even small flagellates of 3 to 5 μ in diameter, it can be taken for granted that it will also retain pelagic larvae 100—500 μ in diameter.

Through the experiments of Fox, Sverdrup, and Cunningham (1937) on *Mytilus californiensis* we know the order of magnitude of the water volume transported through the gills per mussel per hour. Adult specimens of the Danish *Mytilus edulis* have an average weight of about 30 g, which according to the results of Fox and collaborators (l. c.) seems to correspond to a water transport of 1.4 l water per mussel per hour. According to Barker Jørgensen (1943) the figures of Fox are probably too small "as the large quantity of lime used in his experiments must mean a severe strain upon the transporting organs, the gills especially". The results based on the calculations of Fox must accordingly be regarded as minimum figures. Let us now regard these figures in relation to the ecological conditions in the innermost areas of for instance the Isefjord (cf. pp. 391—392). Here *Mytilus edulis* covers large areas of the bottom and is one of the main competitors. When the larval season is at its height (in late May and early June) about 3000 larvae (dominants: *Mytilus*, *Mya*, *Littorina*) are found per litre of water evenly distributed from the surface to the bottom (at 4—5 m depth). Thus a single adult *Mytilus edulis* filtering about 1.4 l of water per hour will during this period retain about 4,200 larvae, i. e. about 100,000 larvae in 24 hours! This filtering of the water, also performed by *Mya*, *Cardium*, and other dominants within the area, will, no doubt, prove to be an essential source of waste especially in such shallow-watered areas (estuaries, fjords) in which enormous larval swarms (short and limited breeding seasons) are crowding in small volumes of water. In the open sea, for instance the Sound or the North Sea, where the larvae are distributed over a much larger volume of water and accordingly much less densely crowded, this factor seems to be of much smaller significance.

The Cirripeds, which "comb" the water by rapid movements of their arms, seem also to play a certain part as enemies of the pelagic larvae. Thus NILSSON-CANTELL (1921, p. 82) is of opinion that the shallow water species among the Balanids feed on plankton. GRUVEL (1853, p. 553) states that Cirripeds mainly feed on Copepods and even Nauplia of their own species. The Adriatic *Balanus perforatus* has been found to contain large numbers of "*Hydrobia* sp. juv.", about $^1/_4$ mm long in their stomachs (KOLOSVARY 1942), and young of this order of size have, no doubt, been pelagic. No estimate of the water volume combed per hour by the individual Balanid specimens seems to be available, but this volume will to all appearance prove to be very large. As brims of Balanids cover large areas of the sea-shore, it seems reasonable to assume that also this category of plankton feeders will take their heavy tribute of the pelagic larvae.

HUNT (1925, p. 581) found "remains of larval molluscs and worms" in the stomachs of marine Amphipods and Cumaceans.

Finally, as to the more benthonic fishes, NORDGAARD (1912, p. 41) mentions *Mytilus* larvae from stomachs of *Centronotus gunellus* and *Gadus virens*, and S. RUNNSTRÖM (1925) observed that large numbers of *Cypris* larvae of *Balanus balanoides* were eaten by *Gadus virens*.

These few and scattered observations on several systematic groups of animals, pelagic as well as benthonic, which feed on pelagic larvae of bottom invertebrates, seem to show that the consumption is of an essential value as a source of waste for the planktonic larvae. KORRINGA (1941), discussing these problems as regards oyster larvae in Holland thinks (p. 146) that about ten per cent of a stock of oyster larvae in the Oosterschelde will perish "probably mainly by animal enemies" during one tidal cycle, and states that "It is my belief that the toll levied by animal depredators is the most important cause of the diminution of the larval herds in the Oosterschelde". The present author has arrived at similar results as regards the waste in pelagic bottom animal larvae in general. The combination of a high temperature and a food supply sufficiently large to meet the requirements of the high larval metabolism at such high temperatures will give rise to a rapid larval development, a shorter stay in the plankton, a shorter exposure to large crowds of voracious enemies, and accordingly a smaller waste. How large a part of the actual waste must be ascribed to the food conditions, how large a part to the enemies, and how large a part to other unknown conditions, are problems to be solved by future investigators.

VII. English Summary.

The present paper on the reproduction and larval development of Danish marine bottom invertebrates has for its object:

1) To describe the mode of reproduction and development and to figure and identify the larvae in the plankton, thus giving, for each species, a synopsis of all the available literature supplemented with the author's own remarks and fresh sketches of living larvae.

2) To ascertain the breeding seasons (indicated by the planktonic larvae) and to study the problems associated with the recruiting of the populations of bottom invertebrates in the Sound.

3) To discuss in broad features the ecology of reproduction and larval development from fertilisation to metamorphosis in order to find and analyse the critical phases to which the enormous waste of planktonic larvae is due.

Technique (pp. 12—23): A "main series", i. e. ten vertical plankton hauls with a stardard hand-net from the bottom to the surface together with temperature measurements, was taken in the Sound (topography and hydrography, pp. 23—25) every two to three weeks from 1936—39 off Ven and from 1941—42 off Helsingør (cf. pp. 12—14 and figs. 1—2). The living larvae taken to the laboratories in Dewar vessels were examined, sketched, counted species for species, inserted in the lists under provisional designations, and gradually identified. "Pump series" (p. 14) have shown the distribution of the larvae in the water column. The larvae have been reared through metamorphosis: in aquaria (pp. 16—17), in "cages" in the sea (p. 18), and, above all, in new-constructed "bottle-collectors" (pp. 19—23), which have yielded excellent results. Supplementary studies in the Sound and in several other localities (cf. fig. 1) have been made.

Synopsis on reproduction and larval development (pp. 26—367) with an index (pp. 519—523). New data for 220 species of bottom invertebrates and figures of 135 species of pelagic larvae from Danish waters are given. The groups studied most intensively are the *Polychaeta, Phoronidea, Prosobranchia, Tectibranchia*, and *Lamellibranchia*. As to the *Echinoderma, Cephalopoda*, and *Crustacea Decapoda* several new data, but only few new descriptions and figures, are given, while the *Anthozoa, Bryozoa, Placophora, Nudibranchia*, and *Cirripedia* have been treated in very broad features only. — Summaries and (or) discussions of the modes of reproduction and development are given for: *Anthozoa* (pp. 28—29, 31—33), *Polychaeta* (pp. 140—146), *Nemertini* (pp. 147 and 149), *Phoronidea* (p. 153), *Bryozoa* (pp. 156—158), *Placophora* (p. 161), *Prosobranchia* (pp. 240—245), *Opisthobranchia* (pp. 272—276), *Lamellibranchia* (pp. 277—279), *Crustacea Decapoda* (pp. 340—42), and *Echinoderma* (pp. 362—367).

The general remarks on the reproduction and larval occurrence of bottom invertebrates in the Sound (pp. 368—416) are based on direct observations of $^1/_4$ million larvae. The occurrence in the plankton of larvae of different groups throughout the year is outlined in the graphs fig. 193, pp. 374—75 (off Ven) and fig. 194, p. 377 (off Helsingør).

Each "main series", i. e. the larval content of a water column covering $^1/_2$ sq.m. of bottom, off Ven comprises on an average 4,000 larvae (vertical hauls from 18—0 m) and off Helsingør 7,500 larvae (vertical hauls from 30—0 m), that is to say, the average number of larvae per cubic metre is almost the same in both localities. As the actual number of larvae found in the brackish Baltic surface layer has proved to be nearly the same off Ven and off Helsingør, the surplus of larvae in the main series from Helsingør as compared with those from Ven falls upon the bottom layer (the Kattegat water). This fact in connection with the hydrographical conditions and with the occurrence, in several species, of only late larval stages in the Sound seem to show that a large proportion of the larvae off Helsingor have been transported to the Sound from the Kattegat (p. 378). This is supported by the pump series. During July—August—September a certain volume of water was pumped up from each metre of the water column and the contents of larvae were identified and counted. Although the Baltic surface layer has its largest content of larvae in June—July—August, the pump series from late July from the Kattegat layer contained twice as large a number of larval species and specimens as from the Baltic layer, and in August—September the Baltic layer comprises only 10 per cent of the whole stock of larvae. These results compared with the main series from other seasons of the year show that in the Sound the larvae in the Kattegat layer constitute the absolutely dominant element in the plankton in regard to species as well as to specimens. Off Helsingør larvae belonging to the Kattegat layer probably constitute more than 90 per cent of the stock of planktonic larvae for the whole year and a large percentage of these larvae originates from parents in the Kattegat.

The fluctuations in the occurrence of the larvae in the Sound from year to year seem partially to be due to the high mortality of shallow water species during severe ice winters (p. 379) and partially to failure of spawning of larger groups of bottom invertebrates in some years (i. a. owing to failing activation of the sperm, cf. p. 381).

A rough calculation seems to show that in the Sound plankton the larvae belonging to epifauna parents are somewhat more frequent as regards the number of specimens, while the number of larval species is almost identical within the two types of biotopes, with a small surplus to the infauna larvae (pp. 396—398).

The relations between maxima of pelagic bottom animal larvae and of phytoplankton in the Sound have been analysed month for month. The larval curves and the curves for the Nanno- and Ultraplankton have proved to be parallel in broad features, but we have no information of the fluctuations of the naked Flagellates, probably one of the main groups serving as food for larval invertebrates (pp. 408—412).

Among the larvae of bottom invertebrates found in the Sound plankton those of the Lamellibranchs constitute 57.3 per cent, those of the Cyphonautes 12.9 per cent, the Prosobranchs 12.5 per cent, the Polychaetes 10.9 per cent, the Echinoderms 1.9 per cent, the Tectibranchs and Ascoglossids 3.7 per cent, and all the other larvae 0.8 per cent of the total stock. As regards the Lamellibranchs, Prosobranchs, and Polychaetes these figures correspond fairly well to the proportions in which the parent species occur on the level bottom and in the epifauna, while the Echinoderms in spite of their great frequency on the bottom constitute only 1.9 per cent of the pelagic larvae. The Echinoderm larvae, however, have proved to be much more sensitive to brackish water than e. g. the larvae of Gastropods, Lamellibranchs, and most Polychaetes, and when carried to the surface and exposed to the brackish water they will perish on a large scale. Of the 103 living larvae of Echinoderms taken in our pump series, 101 were found in the Kattegat layer, while the lowermost metres of the northward-flowing Baltic layer contain rather large numbers of dead Echinoderm larvae partially in dissolution. The small percentage of living Echinoderm larvae actually occurring in the Sound plankton and consisting mainly of older larvae near the stage of metamorphosis must be regarded as the last laggards of a large larval stock spawned by parents in the Kattegat.

The spawning seasons in the Sound (pp. 400—408), after a minimum in February and March, set in with a small spawning in April—May comprising a few larvae of deep-water species and of pronounced shallow-water species. The first large spawning of the year, the summer spawning (the "Baltic spawning") in June—July—August is characterised in the plankton by numerous specimens of a few species of larvae belonging to shallow water parents (*Mytilus, Mya, Macoma, Littorina*). Then follow, from the middle of June to the middle of August, larvae of species living at intermediate depths, i. e. species with long spawning seasons, because owing to the rise of the temperature the stock living at smaller depths are induced to spawn earlier than the stock living in deeper water. Finally, in August—September, the first phase of the large autumn spawning (the "Kattegat spawning") sets in, characterised by larvae (rather few specimens but a large number of species) of deep-water parents. The second phase of the autumn spawning in December—January, comprising large swarms of a few species of larvae (*Mya truncata, Nephthys ciliata*), after an acute maximum decreases rapidly towards the pronounced minimum in February—March. The table on p. 403 gives the season of larval occurrence for a number of common invertebrate species in the Sound and shows that from spring towards autumn and early winter spawning proceeds gradually from more shallow towards deeper water according to the rise in temperature. The number of larval species is largest in September—October (fig. 196, p. 400) when laggards from the summer spawning are still present and the autumn spawning is at its height. Thus the Sound is characterised by several different spawning seasons in the course of the year, in contrast to the shallow-watered Danish fjords (the Limfjord, Ringkobing Fjord, Isefjord) which have only one large spawning a year, viz. in late spring or early summer (cf. the graphs fig. 198, p. 404). The number of larvae per water volume in spring and early summer is accordingly much larger in the fjords just mentioned than in the Sound (in the Isefjord in late May up to 16 million larvae in a water column covering 1 sq.m. of bottom and in July—August—September on an average 16 times as many larvae over 1 sq.m of bottom in the Isefjord as in the Sound).

The recruiting of the animal stock of the Sound (pp. 413—416). About one-third of all the species of bottom invertebrates in the Sound have a very short pelagic life or a non-pelagic development. Such populations are, of course, recruited by young originating from parents within the Sound itself. About two-thirds of all the species of bottom invertebrates in the Sound have a long pelagic larval life and their populations are mainly recruited from outside areas, viz. from the Baltic and from the Kattegat. The Baltic current removes all or most of the young pelagic larvae produced in the surface layer of the Sound itself, to replace them by a depauperated number of older larvae produced in the Baltic. The Kattegat current carries all or most of the larvae produced in the bottom layer of the Sound southwards (where several of them will perish when exposed to the brackish surface layer) to replace them by a rich supply of mostly old larvae derived mainly from parents living in the southern and middle parts of the Kattegat. — A pelagic larva spends in summer on an average 3 weeks and in winter 1—3 months in the plankton, and several larvae may metamorphose in mid-water if forced to do so (cf. pp. 466—67), afterwards continuing their pelagic life for up to one month.

Such larvae with a prolonged pelagic life are regularly carried to the Sound from northern Kattegat and the Skagerrak, especially in the summer and early autumn when the southward-moving bottom current is strongest, and it is not excluded that even larvae from the North Sea may on certain favourable occasions contribute to the invertebrate stock in the Sound. — A "main series" comprising the larval contents of a water column covering $^1/_2$ sq.m. of bottom is, however, so small as compared with the total water area of the northern and middle parts of the Sound (800 sq.km N. of Taarbæk—Barsebäck) that a single larva found in a main series corresponds, on an average, to more than $1^1/_2$ milliard larvae in the whole area on the particular date. The adults of for instance the Echinoderms *Ophiopholis aculeata* and *Ophiura robusta* are common in the Sound, but their larvae, though known to be pelagic, have never been taken in our main series, and the larvae of several other species common in the Sound as adults were only taken in one, two, or three specimens during our four years' regular collecting. On the other hand our main series comprise several species of pelagic larvae hitherto unknown as adults in the Sound. This shows that the dominant larvae as well as such larvae (or young metamorphosed in mid-water and afterwards continuing their pelagic life) as are of very "rare" occurrence in our main series must be assumed to occur in milliards all over the Sound. No doubt they all occur in sufficiently large numbers to recruit a population on the bottom provided that conditions are favourable for their metamorphosis and settling.

Some outlines of the ecology of reproduction and the larval development of marine bottom invertebrates.

The modes of fertilisation (pp. 417—19 and 443—46) are discussed and analysed. Examples of copulation and "pseudocopulation" and of males and females sitting close together while emitting eggs and sperm freely in the water are given. For species spawning their eggs and sperm freely in the water masses without crowding during the spawning process examples have been found which show that the females, though ripe, will not normally spawn until they are surrounded by a "milieu of sperm" of their own species. In other cases "epidemic spawning", i. e. simultaneous spawning of all the specimens of a large population, is known to take place. These phenomena, that the males are the first to spawn and thus stimulate the females to shed their eggs, or that a whole population has an "epidemic spawning", must be regarded as an ecological rule for species which shed their sexual products freely in the water.

The modes of spawning (p. 419) are discussed, and examples of viviparity, brood-protection, "false brood protection", eggs laid in capsules or gelatinous masses and attached to a substratum, eggs shed singly and adhering separately to a substratum, and eggs shed singly and developing suspended in the water masses, are given.

The spawning inducements (pp. 421—425) which start the spawning in the first males or the "epidemic spawning" in a whole population are discussed. While the food conditions are of little or no value as direct inducers of spawning, the temperature of the sea, as is well known, must be regarded as the main factor controlling breeding in marine invertebrates. Examples are given from the Sound, and it is suggested that the sea-temperature required for an inducement to spawn seems to be another than that required for ripening of the sexual products. — In some Danish fjords poor food conditions will restrict the period of larval development to only a minor part of the period during which the temperature is above the "breeding point". In some high-arctic fjords the temperature is of no influence at all as a direct inducer of spawning in marine invertebrates. Considering this fact in connection with experience gained from other marine invertebrates, i. a. that extracts of algae may induce spawning in ripe Lamellibranchs, it seems probable that an increase in the stock of phytoplankton may induce spawning in marine invertebrates. If so, it is of interest to know whether the phytoplankton only induces spawning in such species (e. g. most Lamellibranchs) as have such a rapid development that already a few days later their larvae will be able to feed on the phytoplankton maximum which induced the spawning of them.

Conditions influencing the length of the breeding season (pp. 425—27) are discussed and examples are given of species with breeding seasons of different lengths (short, long, or throughout the year). Long breeding seasons in a species may be due to: a great vertical range of a population, specimens in shallow water being induced to spawn earlier than such in deeper water according to the rise of the temperature; different spawning times for older and younger specimens (e. g. old specimens or first generation in the spring, young specimens or second generation later in the year); and several spawnings of the same specimens (often rhythmically, connected with the lunar phases).

Species with more than one type of reproduction at their disposal (pp. 427—29) attain an adaptability which enable them to prevail over larger areas of the seas than species with only one mode of reproduction. An analysis and discussion of *Actinia, Spongia, Echinoderma, Polychaeta, Gastropoda, Lamellibranchia, Cephalopoda,* and *Crustacea* have shown that a great variability in the mode of reproduction is found in *Actinia, Spongia* and especially in the ***Polychaeta,*** but is of little significance in the other groups.

The mode of development of the embryos (pp. 429—31). No connection would seem to exist between the mode of oviposition and the mode of development in marine invertebrates. Viviparous species have mainly a non-pelagic development, but the embryos may hatch as pelagic larvae (foreign seas). Some species with brood-protection as well as some which lay their eggs in capsules or gelatinous masses may hatch as pelagic larvae, while others hatch as non-pelagic young. Eggs shed singly and attached separately to a substratum have mainly a non-pelagic development (pelagic in *Aporrhais*). Nearly all eggs shed singly and suspended in the water will develop into larvae with a long pelagic life (non-pelagic in *Arenicola, Amphitrite,* and *Thelepus*). Most embryos with a non-pelagic development originate from large yolky eggs, others from eggs surrounded by a white-like substance or a gelatinous jelly which serves as their food. When occasionally twin-embryos have to feed on a supply of white normally at the disposal of a single embryo, the development may change from non-pelagic to pelagic. Several non-pelagic young feed on "nurse-eggs", i. e. eggs (of such a size as in other species are normally found to develop into pelagic larvae), which are laid several together within a common space, where only a few of them will develop, not hatching until they have devoured all the other eggs, the "nurse eggs", in the space. Embryos feeding on large numbers of nurse eggs will always develop in a non-pelagic way, while embryos feeding on a few nurse eggs only (e. g. *Natica catena*) may vary from a pelagic to a non-pelagic development in accordance with the (not constant) number of nurse eggs at the disposal of the individual embryo. Prosobranchs in foreign seas may reproduce by pelagic larvae in one locality and by nurse eggs and non-pelagic young in another, and some Polychaetes in our seas may reproduce by pelagic larvae or by nurse egg-feeding embryos, varying with the seasons of the year.

Three types of pelagic larvae are known: Planktotrophic larvae with a long pelagic life, planktotrophic larvae with a short pelagic life, and lecithotrophic larvae (pp. 431—38).

The planktotrophic larvae with a long pelagic life (pp. 432—35) originate from small eggs poor in yolk, i. e. they are "cheap" to produce and are accordingly produced by females, often only one year old, on a large scale. Their long pelagic life and their enormous numbers give them chances to spread, to settle in new water areas, and to found new populations. Their growth and development, however, depend entirely on the production of phytoplankton, and years with poor food conditions may mean a catastrophe to a whole stock of larvae. This long pelagic life also means a heavy toll levied by their enemies, i. e. a large waste. — Larvae of this type, rare or absent in arctic seas and in the deep sea, are found in nearly two-thirds of the invertebrates in the Danish waters, and their dominance is still more pronounced in the tropical coastal waters. Apart from the special organs (ciliary rings, velum, etc.) serving in the larval locomotion the Polychaete, Prosobranch, and Lamellibranch larvae of this type exhibit features very similar to their parents, while the Echinoderm larvae are totally different from their adults with a "gap" between the larval stage and the bottom stage.

The planktotrophic larvae with a short pelagic life (pp. 435—36) have these features in common: their size and organisation are the same, or very nearly the same, at the moment of hatching and the moment of settling. For larvae of this type, feeding on plankton seems to be of secondary importance, the spreading of the larval stock being the main object. Such larvae seem to constitute a rather small proportion (less than 10 per cent) of the invertebrate species in all seas, arctic as well as temperate and tropical.

The lecithotrophic pelagic larvae (pp. 436—38) in most cases originate from large yolky eggs which develop into clumsy larvae rather unfit for active locomotion. They take no food from the plankton, feeding exclusively on the content of yolk in the egg cell from which they originate. Their chance to reach the stage of metamorphosis is accordingly much more stable than that of planktotrophic larvae, and, like these, they may take advantage of the water masses to spread over wide areas. — The number of eggs spawned per female is, however, rather small, and the relatively few larvae have only small chances of prevailing in years with good food conditions. Such larvae seem to constitute a rather small percentage of invertebrate species in temperate and warm seas, but are apparently absent from high-arctic seas.

The "waste" of larvae during the pelagic life (pp. 438—46). Quantitative investigations on Danish invertebrates in selected localities during a series of successive years have revealed large fluctuations in number and weight from year to year for several common species, while other common species have shown a rather great stability of occurrence in the same years and in the same areas. A closer analysis seems to show that species with great fluctuations from year to year have planktotrophic larvae with a long pelagic life, while species with a great stability of occurrence have a very short pelagic life or a non-pelagic development (cf. fig. 199, p. 439). There can hardly be any doubt that we are here concerned with one of the main causes of the fluctuations in the quantity of "fish-food" which is of such immense significance to practical marine biology.

The number of eggs produced by the individual species (pp. 440—43). In such sea areas as have been under scientific control for a long time, e. g. the Sound, the total fauna seems to undergo only small alterations during long periods. The species reproducing there seem to be "in equilibrium", and the various modes of development, whether non-pelagic, planktotrophic, or lecithotrophic, seem to serve their purpose in all the species which use them, viz. to maintain the population and to ensure to the individual species their normal percentage share in the invertebrate stock on the bottom. Each pair of spawning animals seems on an average to produce precisely that number of eggs and larvae which will suffice to ensure the growth to maturity and spawning of another pair of specimens of the next generation. Species with a larger number of eggs have, therefore, a larger "waste" of eggs and larvae than those with a few eggs only. The figures hitherto known for the number of eggs produced per female per season as compared with the mode of development, clearly show that the greatest waste takes place during the planktotrophic pelagic stage. A comparison of the egg number per year per female of species belonging to the same genus and living in the same area and with different modes of development (e. g. *Littorina littorea* (long pelagic, planktotrophic life), *L. obtusata* (non-pelagic development), and *L. saxatilis* (viviparous)) will give valuable information about the amount of this waste. Such information may also be obtained from "nurse egg feeders". The North Atlantic prosobranch *Volutopsis* normally uses 50,000 to 100,000 nurse eggs for feeding a single embryo. The frequency and rather wide distribution of this species seems to show that this mode of development functions well. As we know species which use all their eggs to produce pelagic larvae in one locality, while the same species use most of their eggs as nurse eggs in another locality, as the nurse eggs are of a size which is normally known to develop into pelagic larvae, and as "nurse-egg feeders" are known to originate from ancestors with pelagic larvae, it seems likely that the number of nurse eggs spent per embryo will be smaller than the number of larvae lost if all the eggs had developed in a pelagic way, i. e. in the case mentioned less than 0.001 per cent would have survived if pelagic.

The waste caused by failing fertilisation of the eggs has been discussed on pp. 443–46. The conjecture previously set forth, that the waste of Echinoderm eggs may partially be due to failing fertilisation owing to inactive sperm weakened by the low pH of the sea water, is disproved and it is shown that there is just as large a waste of eggs and larvae in groups which must be assumed to have a high percentage of fertilisation because copulation takes place. Thus the waste of eggs through failing fertilisation seems to be small and can hardly be reckoned among the critical phases of the larval development.

The food problems of the pelagic larvae (pp. 446—450) are dealt with. An analysis of the food requirements of the different groups of pelagic larvae is given. On the basis of 1) the diameter of the larval oesophagus, 2) the food actually found in stomachs and intestines, and 3) the microorganisms used as food in successful rearing experiments, the type and size of the organisms used as food for larvae of the different systematic groups are outlined. The food value of the different phytoplankton organisms has been compiled from the scattered but comprehensive literature, with a mention of their size and of the larvae known to feed on them. It is shown that the majority of the pelagic larvae of bottom invertebrates feed on Nanno- and Ultraplankton, and, apart from a few exclusively carnivorous larvae, also such larvae as may feed on animal food and on large diatoms are able to feed exclusively on Nanno- and Ultraplankton, being thus actually "omnivorous larvae".

The duration of the planktotrophic pelagic life is discussed on pp. 451—457. Examples are given to show that the larval development may vary considerably within a single species according to the environment. The influence of the food, of the temperature, of substances furthering metamorphosis, and of the presence or absence of a suitable substratum on the length of the pelagic life is mentioned, and the conclusion is drawn that it is the shortest periods of pelagic development in culture dishes which correspond most closely to the natural conditions. From the table on p. 453 it is inferred that in northern seas the pelagic development of the summer-breeding species will on an average take about three weeks and that of winter-breeding species from one to two or even three months. The table on p. 456, based upon Echinoderm larvae, shows that larvae living in seas with higher temperatures would seem to require just as long a time for their development as those living in the northern seas.

The adaptability of the pelagic larvae to the temperature, food conditions, and salinity is discussed on pp. 457—460. *Nassa* larvae may starve without dying for at least five days. Young and larvae of *Mytilus* exposed to different conditions in culture dishes and in nature for a period of six weeks showed a variation in volume from 1 (poorest conditions) to 4000 (best conditions), but even the smallest specimens found after the experiments were in good health.

Phototaxis and vertical movements of the larvae (pp. 460—63). Examples gathered from the literature show that larvae of Polychaetes, Nemertines, Prosobranchs, and Crustaceans are photopositive in their youngest stages, but change to photonegativity on approaching the stage of metamorphosis. This seems to be an ecological rule. Only such species as live as adults in the tidal zone are photopositive also in their last larval stage.

Choice of a substratum (pp. 463—66). It was formerly supposed that metamorphosing larvae which happened "by chance" to fall on a suitable substratum would survive, while such larvae as by the same "chance" settled on a substratum which was unfit for their future life would perish. The recent literature has shown that late larvae may settle at once when they find a suitable substratum but are able to postpone their metamorphosis from a few days to several weeks if no suitable substratum is found. During this period the larvae which are "forced" towards the bottom by their photonegativity will "test" the bottom at short intervals. When such a larva floats along the bottom with a current with a velocity of for instance half a knot, it will be able to test the sea-bottom along a distance of c. 170 km in one week, i. e. it would seem to have a good chance of finding a suitable substratum and the waste sustained during metamorphosis seems to be much smaller than previously assumed.

Larvae metamorphosing in mid-water and afterwards continuing their pelagic life (pp. 466—67) were found regularly in our main series though they were only present in few and scattered specimens. They seem to be most frequent among the Echinoderms, but examples are given for Polychaetes, Prosobranchs, and Opisthobranchs also. It is suggested that the "Benham stage" in *Arenicola* should be regarded as such a mid-water metamorphosis. These "pelagic bottom stages" are of no little importance for the spreading of the species.

The pelagic larvae and their enemies (pp. 468—71). The analyses recorded in the present paper seem to show that the main conditions causing the enormous waste of the planktotrophic pelagic larvae are probably different from those which have hitherto been regarded as the most essential. The immense number of eggs per female with planktotrophic pelagic larvae as compared with the rather small number of such with lecithotrophic pelagic larvae shows that the food is of great value as a limiting factor. — The most important single factor causing the waste seems, however, to be the enemies. Examples are gathered to show the large number of animal species, from Protozoans to Fishes, planktonic as well as benthonic, which feed partially or exclusively on pelagic invertebrate larvae. Attention is called to the large waste of larvae in shallow-watered areas during the main breeding season, when the larvae are densely crowded within a rather small volume of water. A single adult *Mytilus* which, like several other bottom invertebrates, retains the larvae contained in the water that passes through its gills may, in the Isefjord, cause the death of 100,000 pelagic larvae in twenty-four hours. Also the volume of water sieved, i. e. the number of larvae caught, by the dense brims of the Balanids along our shores would seem to be considerable. — On this as on most of the other points discussed and analysed above fresh information and supplementary observations are highly desirable.

VIII. Dansk Resumé.

(Til Forklaring af det følgende skal anføres, at man ved Plankton forstaar alle Dyr og Planter, der tilbringer deres Liv svømmende eller svævende i de frie Vandmasser. Saadanne Dyr kaldes ogsaa planktoniske eller pelagiske).

Denne Afhandling beskæftiger sig med Forplantningen og Larveudviklingen hos de lavere Bunddyr i danske Farvande, deriblandt ogsaa et stort Antal af de Dyr, der udgør Fiskenes væsentlige Føde. Undersøgelsens Formaal har været:

1. At beskrive Forplantningen og Udviklingen og at afbilde og bestemme de ofte ganske ukendte Bunddyr-Larver i Planktonet. Ved at fremdrage den hidtil kendte Litteratur om Forplantning og Udvikling for hver Art, suppleret med nye Iagttagelser og nye Skitser af de levende Larver, at skabe en Haandbog over Forplantning og Larveudvikling hos nordiske Bunddyr.
2. Gennem Larvernes Optræden Aaret rundt i Øresunds Plankton at belyse specielle Forhold i dette Farvand og udrede, hvorfra de voksne Bestande paa Havbunden rekrutteres.
3. I grove Træk at give en Oversigt over de forskellige Faktorers Indflydelse paa Forplantningen og Larveudviklingen fra Æggenes Befrugtning og Gydning til Larverne forlader Planktonet og gaar over i Bundstadiet. Denne nye Videnskabsgren — "Larveøkologien" —, af hvilken en samlet Fremstilling ikke tidligere har været givet, omfatter bl. a. en Analyse af de kritiske Faser under Udviklingen, for at finde Aarsagen til det vældige Svind af Larver under denne.

Teknik: Fra smaa Laboratorier paa Øen Ven og i Helsingør blev der med 2—3 Ugers Mellemrum Aaret rundt fra 1936—39 (Ven) og fra 1941—42 (Helsingør) taget regelmæssige Planktonprøver — "Hovedserier" — d. v. s. 10 lodrette Træk fra Bund til Overflade med et Standardnet. De levende Larver blev i Thermoflasker bragt til Laboratoriet, hvor Optælling, Tegning og Bestemmelse fandt Sted. For at finde Larvernes Fordeling i Vandsøjlen suppleredes "Hovedserierne" nu og da med "Pumpeserier", hvor 100—200 Liter fra hver Meter af Vandsøjlen pumpedes op og undersøgtes for Larver. Blandt de mange Metoder, der benyttedes til Bestemmelse af Larverne, skal her særlig nævnes den til Formaalet konstruerede "Flaske-Samler" (beskrevet og afbildet Side 19—23), som alene paa een Sommer skaffede os Forvandlingsstadier af ca. 70 Arter af Bunddyrlarver og som har givet helt nye Muligheder for at bestemme saadanne Arter, som er vanskelige at holde i Akvarium.

Haandbogen over Forplantning og Larveudvikling hos nordiske Bunddyr omfatter Side 26—367 med et Register Side 519—523. Den giver bl. a. nye forplantningsbiologiske Data for ca. 220 Arter af Bunddyr og omfatter ca. 700 originale Enkeltfigurer bl. a. af 135 Arter af planktoniske Bunddyrlarver tegnet levende med Abbe's Tegneapparat. Desuden gives et Resumé med Litteraturhenvisninger af alle tidligere Observationer vedrørende Forplantningsbiologien for hver enkelt Art. Flest nye Data findes indenfor Grupperne Børsteorme, Forgællesnegle, Baggællesnegle og Muslinger, men ogsaa Pighude, Blæksprutter og Storkrebs er grundigt gennemgaaet, mens Grupper som Koraldyr, Mosdyr, Slimbændler og Rankefødder er behandlet i meget grove Træk.

Det er velkendt at Øresund omfatter 2 Vandmasser: Østersøvand d. v. s. brakt Overfladevand, der løber mod Nord, og Kattegatvand d. v. s. salt Bundvand, der løber mod Syd, men standses og tvinges op mod Overfladen af den undersøiske Højderyg ("Tærskel") mellem Amager og Limhamn, hvor det blandes med Østersøvandet og føres nordud gennem Sundet. Hvad Østersøvandet angaar, er Øresund saaledes et "Sund", hvad Kattegatvandet angaar kun en "Fjord". I Sundets nordlige Del blandes disse Vandmasser kun i ringe Grad. Lodrette Maalinger gennem Vandmasserne viser ofte et skarpt "Spring" i Temperatur og Saltholdighed ved Overgangen fra det ene Vandlag til det andet. Dette "Springlag", der skiller de 2 Vandmasser, skiller ogsaa deres Bunddyr-Bestande og deres Larver. Medens Overfladen er meget brak og har et fattigt Dyreliv, er det dybe Vand meget salt (ligesaa salt som paa samme Dybde N. for Læsø) og har en artsrig Fauna. Det brakke Overfladevand tvinger Lavtvandsdyrene ned paa dybere Vand, og Bundstrømmen fra Kattegat tvinger salt Vand fra den dybe østlige Kattegatsrende og dermed dennes Dyreliv op paa meget mindre Dybder i Sundet, saaledes at vi i Øresund fra ca. 15—35 m Dybde har en Fauna, der i alt væsentligt svarer til Faunaen i det nordlige Kattegat fra 0—70 m. Denne "lodrette Koncentration" af Dyrelivet gør Sundet mere end dobbelt saa rigt paa Arter som Storebælt, hvor Bundvandet er mindre salt. Fra Sundet kendes 32 Arter Pighude, 61 Arter Muslinger, 110 Arter Snegle og 143 Arter Børsteorme, gode Eksempler paa den store Rigdom af Arter.

Vore Undersøgelser har vist, at langt det største Antal af Bunddyrlarverne i Øresunds Plankton (over 90 $^0/_0$ ved Helsingør og betydeligt over 50 $^0/_0$ for hele det nordlige Øresund) findes i Kattegatvandet. Det store Antal af ældre Larver i Kattegatslaget viser, at en meget stor Procent af disse Larver er ført til Sundet udefra d. v. s. stammer fra Forældre i Kattegat. Det for nogle Arter stærkt varierende Antal Larver i Sundet fra Aar til Aar synes forklaret dels ved den høje Dødelighed af Lavtvandsdyr under strenge Isvintre, dels ved at Gydning hos de paagældende Arter nu og da helt eller delvis udebliver (bl. a. paa Grund af inaktive Sædfim).

I Sundets Plankton er Larver af "Epifauna-Dyr" (d. v. s. Dyr knyttet til Vegetation, Sten eller Skalbanker) de hyppigste i Individantal, medens Larver af "Infauna-Dyr" (d. v. s. Dyr knyttet til den jævne Havbund) har en lille Overvægt med Hensyn til Artsantal. Der synes i grove Træk at være god Overensstemmelse mellem Bunddyrlarvernes Optræden i Sundets Plankton og Mængden af deres Føde, d. v. s. de mikroskopiske Planteplankton-organismer, der gaar under Betegnelsen Nanno- og Ultraplankton. Dog mangler vi Kendskab til de nøgne Flagellaters Optræden Aaret igennem, og disse er antagelig en vigtig Fødekilde for Bunddyrlarverne. Blandt Sundets planktoniske Bunddyrlarver udgør Muslingerne 57,3 $^0/_0$, Mosdyrene 12,9 $^0/_0$, Forgællesneglene 12,5 $^0/_0$, Børsteormene 10,9 $^0/_0$, Baggællesneglene 3,7 $^0/_0$, Pighudene 1,9 $^0/_0$ og alle andre Larver tilsammen 0,8 $^0/_0$. For de fleste af disse Grupper svarer Procenten ganske godt til, hvad man maatte vente efter de voksne Dyrs Hyppighed paa Bunden. Kun for Pighudene, der er meget talrige paa Bunden og næsten alle har fritsvævende Larver, er den lave Larveprocent forbavsende. Forklaringen maa søges i, at Pighudelarverne er særlig sensible overfor Brakvand og dør i stort Antal, naar de ved "Tærsklen" Amager—Limhamn tvinges op i det brakke Østersøvand. Af 103 levende Pighudelarver i vore "Pumpeserier" fandtes de 101 i Kattegatsvandet, medens de nederste Meter af det brakke Østersøvand indeholdt et stort Antal døde, halvt opløste Pighudelarver, som drev nordpaa ud af Sundet. Sundets egen Bestand af Pighudelarver gaar paa denne Maade til Grunde i en ung Alder i endnu langt højere Grad end Larverne af de andre Grupper, og den lille Procent af Pighudelarver i vore "Hovedserier" maa betragtes som de sidste Efternølere fra en Larvesværm, der er produceret i Kattegat, og derpaa ført sydpaa ned mod Sundet.

Gydningen i Sundet begynder, efter et Minimum i Februar—Marts, ganske svagt i April—Maj med Larver af baade Dybvands- og udprægede Lavtvandsarter, men den første store Gydning — Sommergydningen eller "den Baltiske Gydning" — sætter ind i Juni, Juli, August. Den bestaar af talrige Larver af nogle faa, almindelige Lavtvandsarter (Blaamusling, Sandmusling, Østersømusling og Strandsnegl). Saa følger — fra Midten af Juni til Midten af August — Larverne af Arter fra Mellemdybderne. De har en lang Gydningssæson, da den Del af Bestanden, der lever paa lavest Dybde, tidligere udsættes for den høje Vandtemperatur, der fremkalder Gydningen, end Bestanden paa dybere Vand. Endelig i August—September begynder Efteraarsgydningen eller "Kattegatsgydningen" karakteriseret ved relativt faa Larver af et stort Antal Arter fra dybere Vand. Første Fase af denne Gydning afsluttes tidligt i Oktober, men næste Fase, med et lille Antal Arter, optræder saa sent som i December—Januar (paa 30—40 m Dybde i Sundet er Temperaturen højest i Slutningen af November!).—Antallet af Larvearter i Planktonet er størst i September—Oktober, da de sidste Larver fra Sommergydningen endnu optræder, medens Efteraarsgydningen er i fuld Gang. Medens Sundet saaledes har Gydningen fordelt over en stor Del af Aaret, har de indre Danske Fjorde kun een koncentreret Gydning pr. Aar, nemlig i det sene Foraar eller i Forsommeren, hvor Larveantallet pr. Kubikmeter Vand ligger uendelig meget højere end i Sundet.

Ca. $^1/_3$ af Sundets Arter af lavere Bunddyr har et meget kort pelagisk Liv eller en u-pelagisk Udvikling, og saadanne Bestande rekrutteres af Larver fra Sundet selv. Ca. $^2/_3$ af Sundets Arter har dog et langt pelagisk Larveliv, og disse Bestande rekrutteres hovedsagelig af Larver fra andre Havomraader: fra Østersøen og Kattegat. Østersøvandet fører de fleste af Sundets egne "Lavtvands-Larver" mod Nord ud i Kattegat og erstatter dem med Larver fra Østersøen. Kattegatvandet fører Sundets egne "Dybvands-Larver" mod Syd, hvor mange af dem dør, naar de ved Amager—Limhamn udsættes for Brakvand, og erstatter dem med Sværme af især ældre Larver gydt i det sydlige og midterste Kattegat. Beregninger over Larvernes Levetid i Planktonet og den sydgaaende Strøms Hastighed har vist, at planktoniske Larver ofte kan naa ned i Sundet fra det nordlige Kattegat og Skagerak, ja undtagelsesvis endog fra Nordsøen. Da vore "Hovedserier" jo kun omfatter Larver fra et uendeligt lille Volumen af Sundets samlede Vandmasse, kan man gaa ud fra, at selv saadanne Larver, der optræder sjældent og i enkelte Individer i vore "Hovedserier", vil findes i Milliarder i Sundets samlede Vandmasser. Vi kender Arter, der er hyppige paa Bunden, og som vides at have pelagiske Larver, men hvis Larver vi aldrig har truffet i vore "Hovedserier", og vi kender et stort Antal Larver fra vore "Hovedserier", der tilhører Arter, som aldrig er taget i Bundstadier i Sundet. Dette sidste viser, at et stort Antal Larver af Arter, der ikke nu kendes fra Sundet som voksne, Aar for Aar tilføres Sundet i saadanne Masser, at de let vil kunne grundlægge nye Bestande fra Bunden, hvis der skulde opstaa gunstige Betingelser for deres Forvandling og Bundfældning.

De forskellige Faktorers Indflydelse paa Forplantningen og Larveudviklingen hos de marine Bunddyr gennemgaas Punkt for Punkt, saaledes bl. a. Befrugtningsmaaderne fra Parring, gennem "Pseudoparring", til frit i Vandet aflagte Æg. Det har vist sig som en økologisk Regel hos Arter, der gyder Æg og Sæd frit i Vandet, at enten gyder Hannerne først deres Sæd, og denne stimulerer Hunnerne til at gyde, eller ogsaa gyder en hel Bestand samtidig ("epidemisk Gydning"). Paa denne Maade opnaar saa godt som alle Æg at blive befrugtede, og Tabet af Æg under Befrugtningsprocessen er langt ringere, end man tidligere har troet.

Gydningsmaaderne fra Levendefødsel og Yngelpleje til Ægkapsler, Ægmasser og frit aflagte Æg gennemgaas, og det diskuteres hvilke ydre Faktorer, der sætter Gydningen i Gang. Temperaturen er den vigtigste Faktor, men der skal en anden og som Regel højere Temperatur til at bringe en Hun til at gyde sine Æg end til at faa samme Hun til at modne dem. Paa visse Lokaliteter f. Eks. i højarktiske Have, kan Gydningen dog foregaa uden Temperaturstigning, men samtidig med (og maaske foraarsaget af) en Stigning i Produktionen af Planteplankton. — Endelig gives en Oversigt over de ydre Faktorer, der betinger Gydningstidens Længde.

Det vises, at medens langt de fleste Grupper af Saltvands-Bunddyr kun har een Forplantningsmaade pr. Art, har Søanemoner, Havsvampe og især Børsteorme den Evne at kunne variere deres Forplantningsmaade (fra pelagisk til upelagisk Larveudvikling o. s. v.) fra Aarstid til Aarstid eller fra Sted til Sted. Dette er sikkert en væsentlig Del af Forklaringen paa Børsteorme-Arternes ofte jordomspændende Udbredelse.

Der synes ikke at være nogen nærmere Forbindelse mellem Gydningsmaaden og Udviklingsmaaden hos marine Bunddyr. Dog synes Æggene hos levendefødende Forældre som Regel at udvikle sig uden fritsvømmende Stadium, medens Æg aflagt frit i Havet ofte bliver til fritsvømmende Larver. Fostre med en upelagisk Udvikling stammer oftest fra store, blommerige Æg, eventuelt omgivet af en æggehvideagtig Substans. Andre Arters Fostre ernærer sig af "Nærings-Æg", d. v. s. Æg (af en Størrelse, der hos andre Arter normalt udvikler sig til pelagiske Larver) lægges mange sammen i et fælles Ægrum, hvor kun nogle faa af dem udvikler sig til Fostre, der først forlader Ægrummet, naar de har fortæret alle de andre Æg: "Nærings-Æggene". Fostre, der ernærer sig af et stort Antal Næringsæg, vil altid have en upelagisk Udvikling, medens Fostre, der kun æder nogle faa Næringsæg, kan variere fra pelagisk til upelagisk Udvikling i Overensstemmelse med det (ikke konstante) Antal Næringsæg til Disposition for det enkelte Foster. — Arter i fremmede Havomraader kan forplante sig med pelagiske Larver paa eet Sted og upelagisk med Næringsæg paa et andet.

De fritsvømmende Larver kan inddeles i 3 økologiske Typer:

A. Planktonædende Larver med et langt fritsvømmende Liv, der stammer fra smaa, næringsfattige Æg, som kan produceres med ringe Stofforbrug og i stort Antal af ofte kun aarsgamle Hunner. Deres lange Levetid i Planktonet og store Antal giver dem gode Chancer for Spredning til nye Havomraader og til at grundlægge nye Bestande her. De er helt afhængige af Planteplanktonet som Føde og kan derfor i daarlige Fødeaar komme ud for Katastrofer, og det lange fritsvømmende Stadium betyder, at en Mængde af dem bliver ædt af Fjender. Denne Type af Larver mangler i Dybhavet, er sjældne i de arktiske Kystzoner, findes hos ca. $^2/_3$ af Bunddyr-Arterne i vore Farvande og dominerer i de tropiske Kystfarvande.

B. Planktonædende Larver med et kort fritsvømmende Liv har omtrent det samme Udseende og Størrelse i Klækningsøjeblikket som naar de forlader Planktonet for at gaa over i Bundstadiet. De kan tage Føde fra Planktonet, men det fritsvømmende Stadium er først og fremmest et Spredningsstadium. Denne Type af Larver udgør en lille Procent (mindre end 10 $^0/_0$) af Bunddyrlarverne i alle Have, arktiske som tropiske.

C. Lecithotrophe Larver (d. v. s. Larver, der uden at tage Føde fra Omgivelserne udvikler sig paa Basis af den Blommemasse, der fandtes i Ægget) stammer fra store næringsrige Æg og har ofte et langt fritsvømmende Liv. Deres Risiko under det fritsvømmende Liv er langt ringere end de planktonædende Larvers, og dog har de Chancer for at spredes gennem Havstrømme. Ægantallet pr. Moderdyr er ret lille, hvad der nedsætter disse Larvers Konkurrenceevne betydeligt. De udgør en forholdsvis lille Procent af Larverne i tempererede og tropiske Kystomraader, men mangler i højarktiske Have.

En Sammenligning mellem vore Erfaringer og Dansk Biologisk Stations Undersøgelser over Variationen af Fiskefødedyr paa den jævne Havbund i vore Farvande har vist, at Arter med store Variationer i Antal og Vægtmængde fra Aar til Aar har planktonædende Larver med et langt, fritsvømmende Liv, medens Arter med en stabil Optræden fra Aar til Aar har et kort, fritsvømmende Larveliv eller gaar lige over i Bundstadiet uden noget fritsvømmende Stadium. Det kan næppe betvivles, at vi her har fundet een af Hovedaarsagerne til Variationerne i Mængden af Fiskeføde paa Havbunden, som er af saa stor Betydning for den praktiske Fiskeribiologi.

"Balancen" i et Farvand hos de forskellige Bunddyr-Arter gennem en længere Aarrække med Hensyn til deres procentvise Antal paa Bunden har vist, at Arter med et større Antal Æg og Larver har et større "Svind" af disse end Arter med kun faa Æg. Vort Kendskab til Ægantallet og Larvebiologien hos de enkelte Arter har endvidere vist, at det største "Svind" altid finder Sted blandt de planktonædende Larver med et langt, fritsvømmende Liv. Der gives Eksempler paa, hvorledes man af Hunnens Ægantal pr. Sæson kan udregne Svindets Størrelsesorden. Hos Former med Næringsæg kan man faa et Begreb om det fritsvømmende Larvelivs Kostbarhed ved at beregne, hvor mange Næringsæg (af en Størrelse, der hos andre Arter bliver til fritsvømmende Larver) en Hun har Raad til at ofre (op til 100.000!) for at undgaa dette fritsvømmende Liv blot hos et enkelt Foster.

Paa Basis af Litteraturen og egne Observationer gives der en Oversigt over Larvernes Føde, hvoraf det fremgaar, at bortset fra nogle faa Rovdyr kan næsten alle fritsvømmende, planktonædende Larver, derunder ogsaa saadanne, der nu og da tager dyrisk Føde, ernære sig udelukkende af ganske smaa Planteplankton-Organismer, det saakaldte Nanno- og Ultraplankton.

En Sammenstilling af Litteratur og egne Iagttagelser viser, at planktonædende, fritsvømmende Larver gennemsnitlig opholder sig 3 Uger om Sommeren og 1—2 eller endog 3 Maaneder om Vinteren i Planktonet. Larver, der udvikler sig i tropiske Havomraader, bruger ved de der herskende Temperaturforhold akkurat lige saa lang Tid til deres fritsvømmende Liv som nordiske Arter i nordiske Have.

Der gives en Række Eksempler paa Larvernes store Modstandskraft overfor ugunstige Forhold: Temperatur, Saltholdighed, Fødemangel o. s. v. Paa Basis af Litteratur og egne Observationer vises det, at unge Larver søger mod Lyset og Overfladen, medens ældre Larver søger væk fra Lyset ned mod Bunden. Kun saadanne Arter, der som voksne lever i Tidevandszonen, søger som ældre Larver stadig mod Lyset.

En ældre Larve, der tvinges bort fra Lyset ned mod Bunden, og som her skal til at gaa over i Bundstadiet, havner ikke, som tidligere antaget, paa et tilfældigt Substrat, hvor den kan klare sig eller maa dø alt efter Substratets Karakter, men er i Stand til at undersøge Substratet og til, hvis dette ikke passer den, at forlænge sit fritsvømmende Liv ofte i flere Uger, under hvilke den med Strømmen føres langs Bunden og "afprøver" denne, indtil den finder den Bundart, der passer den. Tabet af Larver ved Forvandlingen og Bundfældningen synes saaledes at være langt mindre end hidtil troet.

Alle disse Betragtninger synes at vise, at det vældige "Svind" under Larvernes fritsvømmende Liv, som faktisk er en Kendsgerning, hovedsagelig skyldes andre Faktorer end de, man hidtil har betragtet som mest væsentlige. Fødemangel er utvivlsomt en vigtig Kilde til "Svind", men den vigtigste Tabsaarsag synes at være Fjenderne, der omfatter alle Havets Dyregrupper lige fra Protozoer til Fisk, fra fritsvømmende Dyr til Bunddyr og fra Larver til voksne Dyr. Det beregnes, at en middelstor Blaamusling med Vandstrømmen gennem sine Gæller paa eet Døgn i Isefjorden kan fra-filtrere og dræbe ca. 100.000 fritsvømmende Bunddyrlarver. Paa disse interessante og vigtige Felter bør Undersøgelser nu sættes ind.

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med store Variationer i Antal og Vægtmængde fra Aar til Aar har planktonædende Larver med et langt, fritsvømmende Liv, medens Arter med en stabil Optræden fra Aar til Aar har et kort, fritsvømmende Larveliv eller gaar lige over i Bundstadiet uden noget fritsvømmende Stadium. Det kan næppe betvivles, at vi her har fundet een af Hovedaarsagerne til Variationerne i Mængden af Fiskeføde paa Havbunden, som er af saa stor Betydning for den praktiske Fiskeribiologi.

"Balancen" i et Farvand hos de forskellige Bunddyr-Arter gennem en længere Aarrække med Hensyn til deres procentvise Antal paa Bunden har vist, at Arter med et større Antal Æg og Larver har et større "Svind" af disse end Arter med kun faa Æg. Vort Kendskab til Ægantallet og Larvebiologien hos de enkelte Arter har endvidere vist, at det største "Svind" altid finder Sted blandt de planktonædende Larver med et langt, fritsvømmende Liv. Der gives Eksempler paa, hvorledes man af Hunnens Ægantal pr. Sæson kan udregne Svindets Størrelsesorden. Hos Former med Næringsæg kan man faa et Begreb om det fritsvømmende Larvelivs Kostbarhed ved at beregne, hvor mange Næringsæg (af en Størrelse, der hos andre Arter bliver til fritsvømmende Larver) en Hun har Raad til at ofre (op til 100.000!) for at undgaa dette fritsvømmende Liv blot hos et enkelt Foster.

Paa Basis af Litteraturen og egne Observationer gives der en Oversigt over Larvernes Føde, hvoraf det fremgaar, at bortset fra nogle faa Rovdyr kan næsten alle fritsvømmende, planktonædende Larver, derunder ogsaa saadanne, der nu og da tager dyrisk Føde, ernære sig udelukkende af ganske smaa Planteplankton-Organismer, det saakaldte Nanno- og Ultraplankton.

En Sammenstilling af Litteratur og egne Iagttagelser viser, at planktonædende, fritsvømmende Larver gennemsnitlig opholder sig 3 Uger om Sommeren og 1—2 eller endog 3 Maaneder om Vinteren i Planktonet. Larver, der udvikler sig i tropiske Havomraader, bruger ved de der herskende Temperaturforhold akkurat lige saa lang Tid til deres fritsvømmende Liv som nordiske Arter i nordiske Have.

Der gives en Række Eksempler paa Larvernes store Modstandskraft overfor ugunstige Forhold: Temperatur, Saltholdighed, Fødemangel o. s. v. Paa Basis af Litteratur og egne Observationer vises det, at unge Larver søger mod Lyset og Overfladen, medens ældre Larver søger væk fra Lyset ned mod Bunden. Kun saadanne Arter, der som voksne lever i Tidevandszonen, søger som ældre Larver stadig mod Lyset.

En ældre Larve, der tvinges bort fra Lyset ned mod Bunden, og som her skal til at gaa over i Bundstadiet, havner ikke, som tidligere antaget, paa et tilfældigt Substrat, hvor den kan klare sig eller maa dø alt efter Substratets Karakter, men er i Stand til at undersøge Substratet og til, hvis dette ikke passer den, at forlænge sit fritsvømmende Liv ofte i flere Uger, under hvilke den med Strømmen føres langs Bunden og "afprøver" denne, indtil den finder den Bundart, der passer den. Tabet af Larver ved Forvandlingen og Bundfældningen synes saaledes at være langt mindre end hidtil troet.

Alle disse Betragtninger synes at vise, at det vældige "Svind" under Larvernes fritsvømmende Liv, som faktisk er en Kendsgerning, hovedsagelig skyldes andre Faktorer end de, man hidtil har betragtet som mest væsentlige. Fødemangel er utvivlsomt en vigtig Kilde til "Svind", men den vigtigste Tabsaarsag synes at være Fjenderne, der omfatter alle Havets Dyregrupper lige fra Protozoer til Fisk, fra fritsvømmende Dyr til Bunddyr og fra Larver til voksne Dyr. Det beregnes, at en middelstor Blaamusling med Vandstrømmen gennem sine Gæller paa eet Døgn i Isefjorden kan fra-filtrere og dræbe ca. 100.000 fritsvømmende Bunddyrlarver. Paa disse interessante og vigtige Felter bør Undersøgelser nu sættes ind.

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